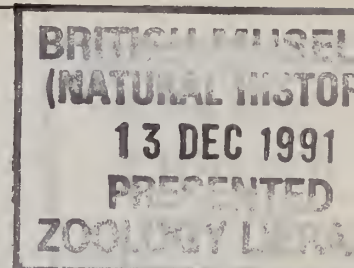# The pharyngobranchial organ of mugilid fishes; its structure, variability, ontogeny, possible function and taxonomic utility.

IAN J. HARRISON

* *Dipartimento di Biologia e Fisiologia Generali, Universita' degli Studi di Parma, 43100 Parma, Italy*

GORDON J. HOWES

Department of Zoology, The Natural History Museum, Cromwell Road, London, SW7 5BD.

CONTENTS

SYNOPSIS. Although a pharyngobranchial organ (PBO) has long been recognised as a characteristic feature of the Mugilidae (grey mullets), little attention has been given to its structure and function. The organ involves extreme modification of the pharyngobranchial bones of the upper gill-arch, their associated musculature and dentition. The skeletal and soft anatomical structures of the adult organ and its development are described. An hypothesis of its function as a filtering and sampling device is put forward. The taxonomic variability of the PBO among mugilid genera is catalogued and its taxonomic and phylogenetic usefulness discussed. An hypothesis of generic-group interrelationships is given based on ontogenetic and sequentially derived features of the PBO.

INTRODUCTION

The Mugilidae, commonly known as grey mullets, includes some 12 genera and *ca.* 80 species which inhabit marine inshore, estuarine, and freshwater environments in tropical, subtropical, and temperate regions of all continents. Mugilids have characteristic oral and branchial filter-feeding mechanisms. Feeding occurs in three ways: the fish forage on the benthos, in a head-down position with the mouth protruded, sucking up the surface layer of deposits which are filtered in the pharyngobranchial cavity; they stir up benthic deposits with their fins, then back into the cloud of suspended particles which are sucked in and filtered; or they selectively browse on aufwuchs (the substrate mat of algal and associated micro-benthic material; see Reid (1985: p. 9) for further description) which covers submerged rock, plant leaf and root surfaces (Günther, 1861; Jordan, 1905; Hiatt, 1944; Ebeling, 1957; Odum, 1968; Hickling, 1970; Fagade & Olaniyan, 1973; Chan & Chua, 1979; King, 1988). A term sometimes applied to mullet feeding is *ilyophagous*, referring to the top-most layer of sediment (Ching, 1977).

Filtration of the selected material is presumably achieved by the gill-rakers in conjunction with a pharyngeal apparatus, referred to here as the *pharyngobranchial organ* (PBO). Given that a filter-feeding mechanism is a principle character of mugilids it is remarkable that so little attention has been given to this organ either anatomically or as a taxonomic character. It is the aim of this paper to redress that situation.

Since Günther (1861) first described the gill-arch feeding mechanism, only Drake *et al.* (1984) and, particularly, Capanna *et al.* (1974) have provided a more complete anatomical and functional description of the system. These authors pointed out that mugilid pharyngeal structures were insufficiently analysed. In our view the PBO holds promise of a character-complex valuable in diagnosing taxonomic groups. Specific and generic level differences appear to be indicated in the gross morphology of various parts of the organ (see below).

Schultz (1946) is the most recent author on generic-level mugilid taxonomy and we have relied on his revision as a basis in making comparisons of various taxa. We have also used an unpublished, but relatively widely circulated, manuscript revision by Ingham (completed *ca.* 1952). Ingham

* Present address: Musee Royal de l'Afrique Centrale, B-3080 Tervuren, Belgium.

attempted a species as well as generic level revision but she, like Schultz, used only a combination of externally visible characters, *eg.*, morphology of teeth and jaw bones, position of nostrils, development of adipose eye-fold tissue, scale type and morphometrics to distinguish taxa. Schultz (1946) recognised 13 genera, 3 described as new, whereas Ingham recognised 11. Trewavas & Ingham (1972) and Trewavas (1973) utilised some of Ingham's unpublished data in their respective reviews.

Few osteological and ontogenetic studies have been made on mugilids. One of us (IJH) is engaged upon a study of mugilid ontogeny and we are confident that there are many, as yet untapped, osteological and other features which will be valuable in discovering and elucidating the interrelationships of mugilid groups.

METHODS AND MATERIALS

Gross morphology of the PBO was studied by removing the opercular bones and cutting away the gill-arches (ceratobranchials) to expose the lateral face of the organ. In specimens of *ca.* 30mm, the organ was stained with haematoxylin which enhances surface features. Internal anatomy was studied by cutting transverse and horizontal sections through the head and by removing the gill-arch *in toto*. Osteological features were examined by using cleared and alcian/alizarin stained specimens. Specimens used are in the collections of the Natural History Museum, London (BMNH) and the Dipartimento di Biologia e Fisiologia Generali, Universita' di Parma (PA). The catalogue numbers of the BMNH specimens examined in this study are given in the Figure legends, and these numbers may be used to retrieve further data concerning localities of capture etc. The PA specimens were all collected from the Mediterranean (mouth of the River Magra, Italy) between 1984 and 1986.

Abbreviations used in text and figures

afb, anterior fat body; av, anterior valve; bc, buccal cavity; bl, Baudelot's ligament; br, brain; cbp, ceratobranchial process; dt, distal teeth; eb1–4, epibranchials (1 to 4); ec, epithelial cushion of PBO; em, ethmoid fat body; epx, epaxial musculature; da, denticulate area; do, dorsal aperture of sulcus; ga1–5, gill-arches (1 to 5); gf, gill filaments; gt, gut; ht, heart; iac, interarcual cartilage; li2, li4, 2nd and 4th *levator internus* muscles; ms, medial septum of PBO; nc, neurocranium; ns3, 3rd neural spine; os, oesophagus; pb1–4, pharyngobranchials (1 to 4); pbk, 3rd pharyngobranchial keel; pbo, pharyngobranchial organ; pcl, *pharyngocleithrales* muscles; pf, pharyngobranchial folds; pfb, posterior (spongiose) fat body; pg pharyngobranchial groove; ppl, posterolateral articulatory process of 3rd pharyngobranchial; ppm, posteromedial articulatory process of 3rd pharyngobranchial; pt, proximal teeth; ptf, pterotic fat body; pv, posterior valve; rdd, *retractor dorsalis* muscle (dorsal section); rdv, *retractor dorsalis* muscle (ventral section); rem, *recti* muscles; rs, rudimentary sulcus; sa, sagitta; sb, sulcus border; SL, standard length; su, sulcus; swb, swimbladder; tp3, tp4, toothplates of pharyngobranchials 3 and 4; tps, strut of toothplate 4; tvs, *transversus* muscle; uh, urohyal; va, sulcal valve; vp, valve precursory folds.

STRUCTURE OF THE PHARYNGOBRANCHIAL ORGAN (PBO)

In those mugilids with a well-developed PBO, it occupies the rear of the pharynx and comprises two hemispherical 'denticulate' cushions. These cushions are separated from each other by a deep cleft in the ventral midline and are cupped ventrally and laterally by the branchial arches (Fig. 1). The relative size of the cushions is such that they occlude the narrow entrance of the oesophagus and, when the mouth is closed and the pharynx compressed, their ventral midline division is occupied by a strong septum joining the 5th ceratobranchials. When the mouth is opened and the buccal floor lowered the septum is withdrawn from between the denticulate cushions.

Externally the PBO comprises a posterolateral cushion formed of thick, stratified, epithelial tissue penetrated by numerous fine teeth (Plate ID & Fig.5C). The size of the cushion and the density of its tissue and teeth are interspecifically variable, but in most taxa the teeth along the ventrolateral and anterior border of the cushion are larger than those on its posteromedial surface (see below). Capanna *et al.* (1974) described the structure of the mucosa as comprising a thick surface layer of stratified epithelium separated by a marked basal membrane from loose, fibrillar connective tissue forming the submucosa. The entire cushion, the pharyngobranchial teeth lying within it and the supporting pharyngobranchial toothplates were referred to by Capanna *et al.* (1974) as the *denticulate area*, a term adopted here (da, in Figures).

Anteriorly, the denticulate area is separated from the 1st gill-arch by a deep channel, the *sulcus* (su), the depth, width, dorsal extension and orientation of which varies between taxa. The rim of the sulcus, formed by the margin of the denticulate area is named the *sulcus border* (sb). Dorsally, the sulcus runs longitudinally and becomes restricted posteriorly into a narrow aperture (do) roofed by the overlying 4th epibranchial (p. 115 and Fig. 1A). The sulcus continues posteroventrally as the deep groove which separates the denticulate (pharyngobranchial) part of the PBO from the internal muscles and fat bodies (Fig. 1A-C). The fold of tissue forming the anterior border of the sulcus is often expanded ventrally into a large flap or *valve* (va). In some taxa there is a single valve large enough to occlude the lower entrance to the sulcus (Fig. 10); in others the valve occurs as a single, small flap halfway along the sulcus, as a pair of flaps, or as small, finger-like projections (Figs 15 & 18).

The aforementioned PBO features situated anterior to the denticulate area appear to correspond to the 'gustatory' and 'mucus secreting' parts of the organ referred to by Capanna *et al.* (1974). These authors mention that in *Liza ramada* two 'plicae' occur where the denticulate part superimposes on the gustatory part. These 'plicae' would seem to correspond to the structures we refer to as valves.

Two large, spongiose *fat bodies* lie medial to the epibranchials and form the core of the organ (Figs 1 & 2). The *anterior fat body* (afb) is between the 2nd and 3rd epibranchials and often surrounds the latter, is covered by the thin wall of the sulcus and in many specimens bulges outward forming a nodule extending into the sulcus. We are not sure whether this is an artifact of preservation or whether, in life, the fat body moves outward when the *levator internus*, which runs
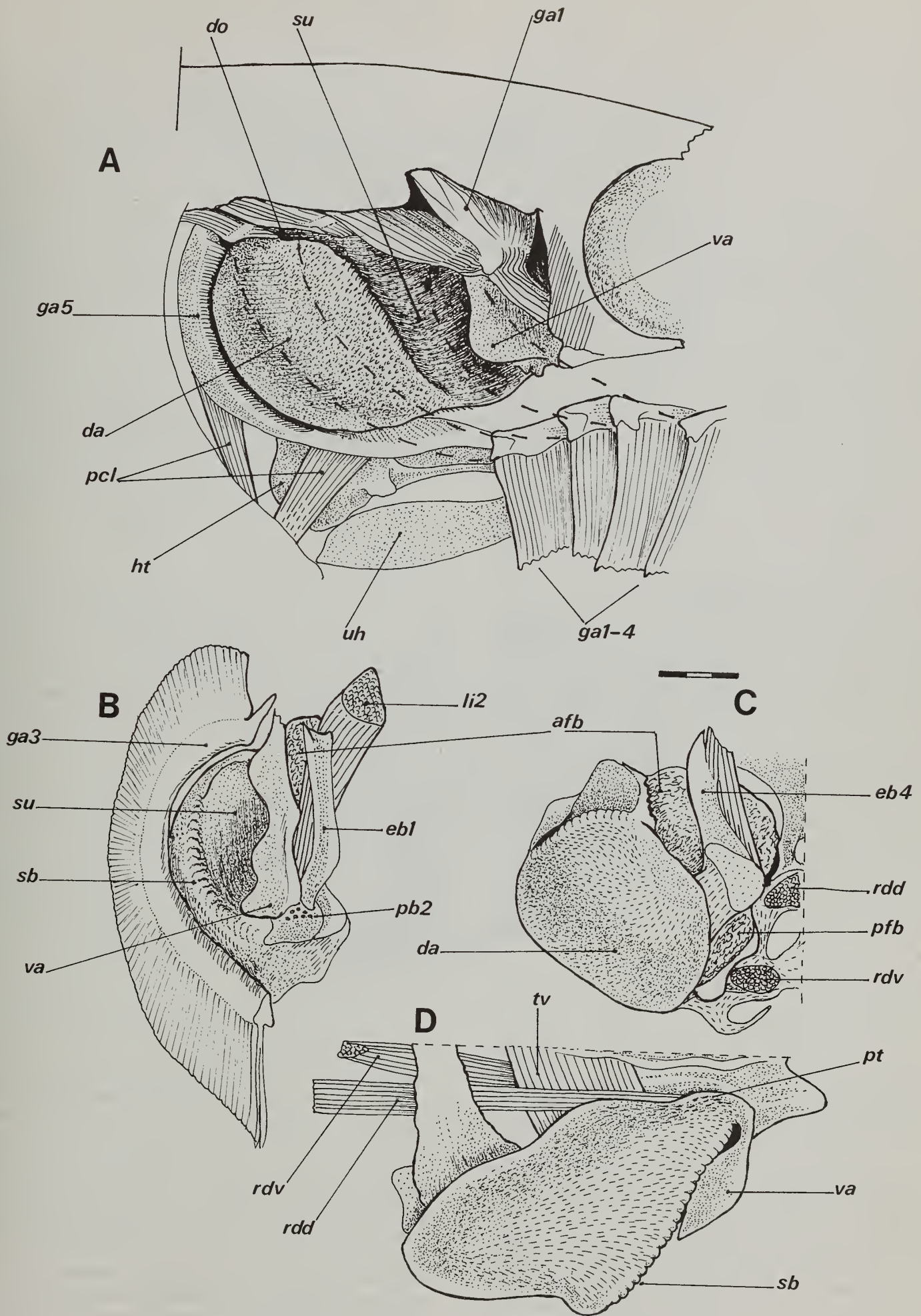
Fig. 1 Position and structure of the mugilid pharyngobranchial organ (*Mugil* sp.). A, lateral view with gill-arches cut away, the dashed lines indicate the position of arches relative to the PBO. B, anterior view of right half of PBO, 1st and 2nd gill-arches have been removed. C, posterior, and D, ventral views of left half of PBO.
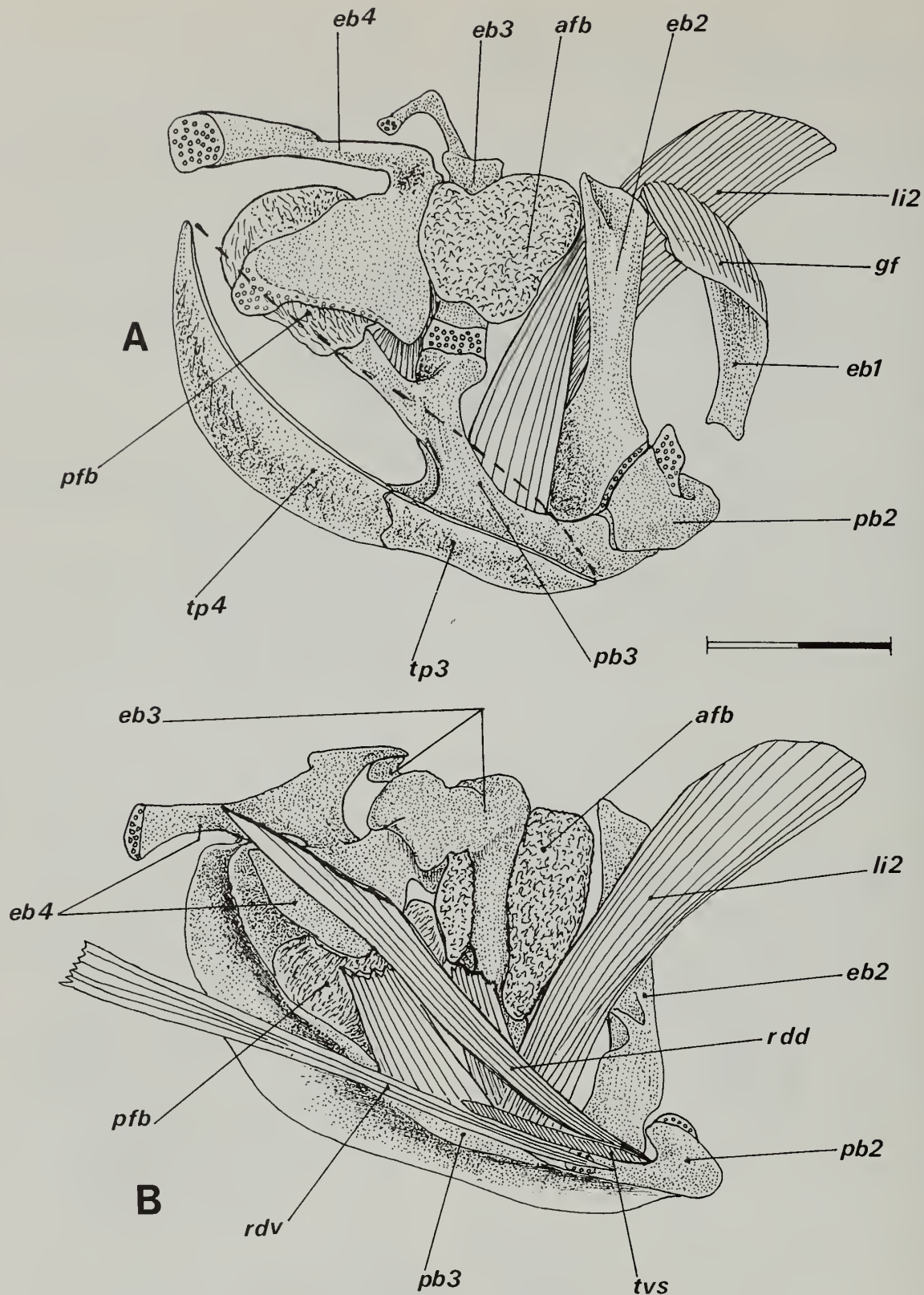
Fig. 2 PBO of *Liza ramada* (BMNH 1949.9. 16: 475–84, 99 mm SL). A, lateral view of right side, most of 3rd and 4th toothplates have been cut away, their dorsal margin shown by dashed line. B, medial view of left half; N.B., 3rd epibranchial surrounded by anterior fat-body.

anteromedial to it, is activated (p. 120). The more spongiose, *posterior fat body* (pfb) lies medial to the 4th epibranchial and a venous blood sinus passes through it.

The *principle muscles* which appear to be directly associated with the functioning of the PBO are the 2nd *levator internus* (li2) which connects the 3rd pharyngobranchial to the sphenotic (in all mugilids), and the *retractor dorsalis* which in the majority of mugilids is divided into distinct dorsal and ventral segments (Fig. 2). The dorsal section of the muscle (rdd) extends from the basioccipital and the ventral section (rdv) from the underside of the vertebral column (usually the 2nd

centrum), with both sections inserting together on the 2nd pharyngobranchial (Figs 1C, D & 2B). In *Agonostomus* and *Joturus* the muscle retains its primitive condition as a single element, originating from the vertebral column, while in *Cestraeus* and *Aldrichetta* only some anterior fibres attach to the basioccipital. *Liza waigiensis* possesses an apparently unique condition in which the dorsal segment of the *retractor dorsalis* originates from a dorsally directed process of the 3rd neural spine (Fig. 3).

The *skeletal framework* of the PBO (Fig. 4) is provided principally by enlarged 3rd pharyngobranchial and 3rd and

4th toothplates; the 4th toothplate is posterolaterally extended to form a long, ventrally convex lamina. Both pharyngobranchial 3 and toothplate 4 are triangular and even in fry of *ca*. 15 mm SL are firmly united in tandem so forming a continuous structure (Fig. 6). The 3rd pharyngobranchial element consists of a fenestrated base-plate to which is attached a large toothplate (Figs 4 & 6). A longitudinal keel (pbk) rises dorsally from the plate to contact anteriorly the 2nd pharyngobranchial and dorsally the 2nd epibranchial. Posteriorly the keel deepens and broadens into two articular processes separated by a foramen in the bone. The medial process (ppm, Fig. 6) extends as a dorsoposterior strut, terminating in an outwardly facing articular head which contacts both the cartilaginous 4th pharyngobranchial and the base of the 4th epibranchial. The lateral process (ppl, Fig. 6) is a vertical pedestal with a flat surface articulating with the base of the 3rd epibranchial. The anterior border of the 4th toothplate rises as a thin, triangular lamina (tps, Fig. 6) adpressed to the inclined strut and vertical pedestal of the respective medial and lateral processes of the 3rd pharyngobranchial. The angles and posterior extent of the lateral and medial processes, and the degree of contact with the border of the 4th toothplate vary within the family.

Two types of *teeth* are associated with the pharyngobranchial toothplates: (1), those similar to the pharyngeal teeth of many other acanthopterygians in being separated from the supporting bone by a narrow collar of poorly mineralised bone (corresponding to the area of collagen described by Fink (1981) as diagnostic of his Type 2 attachment mode). These are referred to as *proximal-type* pharyngeal teeth (pt, Plate IA, C & Fig. 5A, B); (2), those in which the tips are distinctly separated from the bone, being borne on long, poorly mineralised shafts so that the tip of the tooth lies level with, or just below the surface of the epithelial cushion. These are referred to as *distal-type* pharyngeal teeth (dt, Plate IB, C & Fig. 5C).

The size and frequency of both types of teeth undergo considerable ontogenetic change (Capanna *et al.*, 1974; also below). In those taxa which lack a complex PBO (eg., *Agonostomus*, *Joturus*, *Cestraeus*, *Aldrichetta*), only proximal-type teeth are present. Furthermore, in these taxa pharyngobranchial 2 also bears such teeth (Fig. 5A; Rosen & Parenti, 1981: fig. 4C). The adults of those taxa with well-developed PBO's, in contrast, appear to lose most traces of proximal-type teeth but have well-developed distal-type dentition (Plate IC & D).

The following descriptions of teeth are based on juveniles of *Liza saliens*, *L. aurata*, *L. ramada* and *Chelon labrosus* of 40–80 mm SL from the Mediterranean. Although some interspecific differences exist (Drake *et al.*, 1984), the taxa have comparable dental ontogenies.

Proximal-type teeth occur only on pharyngobranchial 2 (in the adults of a few genera (Fig. 5A) and the juveniles of all others, pp. 115 & 119) and in a narrow band along the median borders of the 3rd and sometimes the anterior part of the 4th pharyngobranchial toothplates. The tips are either ankylosed directly with the plate or narrowly separated from it by a ring of poorly mineralised bone. Distal-type teeth cover greater parts of both toothplates. Each tooth is a long stem or shaft of poorly mineralised bone containing a cavity and terminating in a curved calcified tip which lies proud with the epithelial tissue of the mucosa covering the toothplate surfaces. The structure of the teeth varies both ontogenetically (Capanna *et al.*, 1974; also below) and spatially over the toothplates

(Drake *et al.*, 1984). Those distal teeth closest to the medial border of the toothplate are relatively short compared with those situated more laterally. The latter are sequentially longer, with more highly calcified tips. (This size gradation is visible in micrographs of *Oedalechilus labeo*; Plate IC & D). However, distal teeth situated on the dorsolateral aspect of the plate are short and lack calcification. Although for the most part the shafts of the distal-type teeth are poorly mineralised, those on the lateral faces of the toothplates have well-ossified bases.

Drake *et al.* (1984: fig. 11) illustrated the directions in which the tips of the distal teeth curve with respect to their positions on the toothplates. Our observations are in agreement in that the teeth tend to form dense swathes with their tips all pointing in the same direction over various regions of the epithelial surface (see Plate ID for this pattern in *Oedalechilus labeo*). However, we observed greater variability in the directions of curvature than shown by Drake *et al.* The anterior teeth tend to have their tips curved anteriorly whereas those on the anterolateral part of the plate curve more anterolaterad and less mesad than shown by Drake *et al.* The posterior teeth tend to curve posteriorly rather than anteriorly.

Capanna *et al.* (1974) documented the tooth types in *Liza ramada*. Their terminology is somewhat confusing, however, when distinguishing between 'juvenile' and 'adult' teeth. The transverse sections through the denticulate cushions (Capanna *et al.*, 1974: figs 5 & 9) show distal teeth at various developmental stages or from different areas of the toothplates. In SE micrographs of the PBO of a juvenile fish (Capanna *et al.*, 1974: figs 12 & 13) the 'adult' teeth to which the authors refer appear to be proximal teeth (they are relatively robust and distributed in a narrow band along the medial borders of the toothplates).

In all taxa examined the 1st and 2nd *pharyngobranchials* are small elements (Figs 4 & 7). The 1st is a rod-like structure lying above the 2nd and sloping backwards with its anterior tip contacting the proximal cartilage of the 1st epibranchial. The 2nd, sometimes bearing proximal-type teeth, is an almost cuboid element abutting the 3rd pharyngobranchial and forming the anteroventral tip of the PBO; the *retractor dorsalis* attaches to it. An interarcual cartilage lies between the 1st and 2nd epibranchials (Fig. 7; also Travers, 1981: fig. 4).

The *epibranchials* are, with the exception of the 1st, complex structures with medial expansions which form the inner wall of the PBO. There is a good deal of intrafamilial variability in epibranchial morphology; for example, compare *Mugil* (Fig. 4) with *Liza* (Fig. 7).

The 1st epibranchial is nearly always slender and flat, inclined at 45° to the vertical and expanded distally where it articulates with the 1st ceratobranchial. The epibranchial bears an uncinate process which in *Mugil* (Fig. 4) is small and blunt, but which in *Liza* (Fig. 7) and *Chelon* is extended and triangular. Medially, the 2nd-4th epibranchials curve steeply ventrad to meet the pharyngobranchials. The 2nd epibranchial is usually scythe-shaped where it contacts the dorsal keel of the 3rd pharyngobranchial. Arising dorsally from the 3rd and 4th epibranchials are large, knuckle-like uncinate processes, that of the 3rd closely opposing that of the 4th (Figs 4 & 7). Epibranchials 3 and 4 articulate basally with the lateral and medial processes of the 3rd pharyngobranchial. The lateral shaft of the 4th epibranchial bridges the posterodorsal rim of the sulcus, and so forms the narrow, tunnel-like dorsal
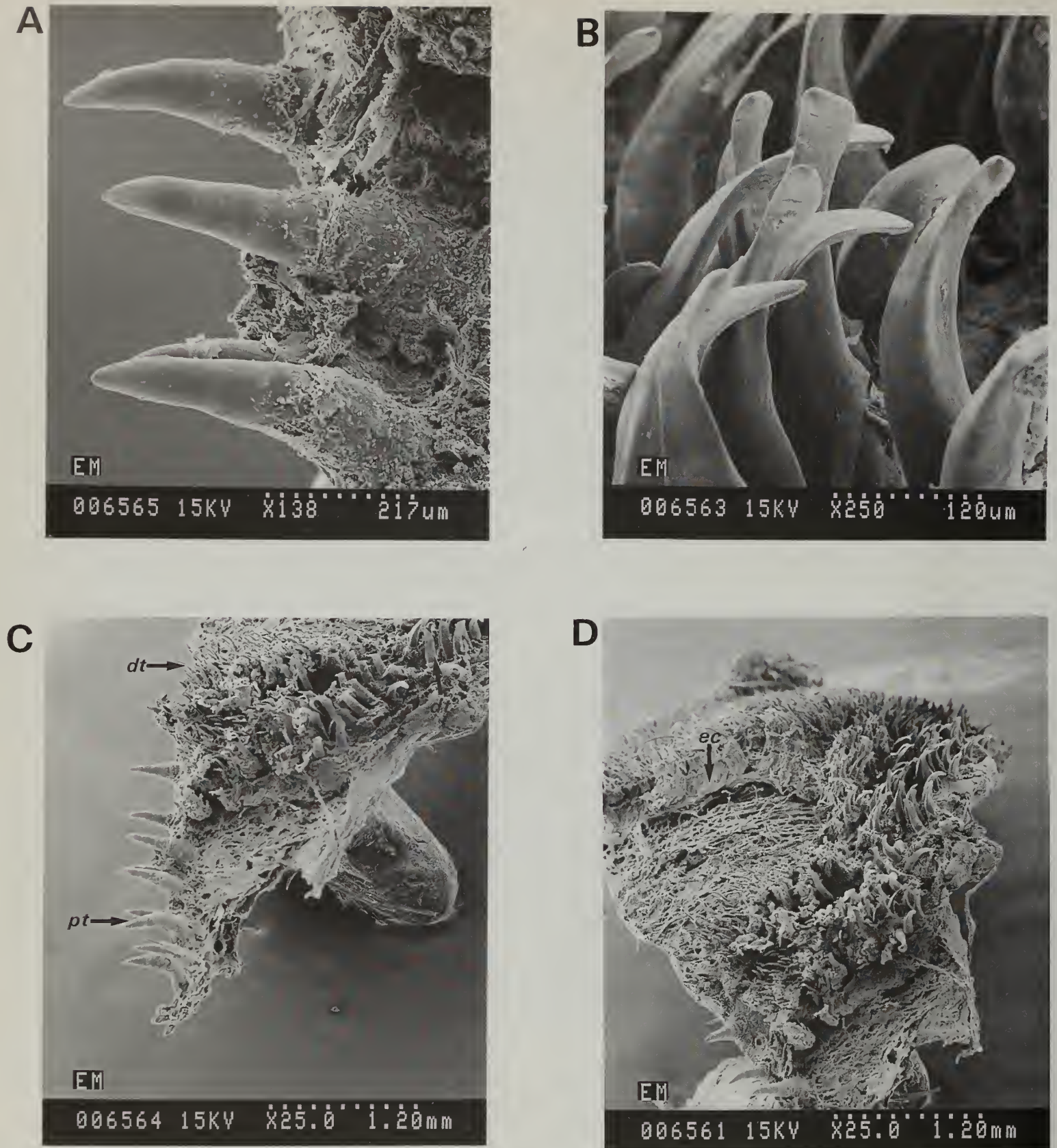
Plate I Scanning electron micrographs of denticulate area of *Oedalechilus labeo* (BMNH 1947.11.2: 1–10, 157 mm SL). A, proximal-type teeth in ventrolateral view; B, distal-type teeth in anteroventral view; C, anterior part of denticulate area in ventrolateral view. Note narrow band of proximal teeth on medial edge, and size gradation of distal teeth from largest situated laterally (arrowed, top-right) to smallest medially (arrowed, top centre); D, entire denticulate area in anteroventral view. Note extensive coverage by various swathes of distal teeth with tips pointing in similar directions, and size gradation from lateral teeth (on right side) to medial teeth (left side). Large central area damaged and devoid of teeth, posterior to this the thick mucosa of the epithelial cushion in which the distal teeth are embedded is visible (arrowed). Scale bars are shown at base of each micrograph.

aperture of the sulcus (Fig. 1A). The 1st and 2nd epibranchials are widely separated from the 3rd and 4th.

The 1st epibranchial bears long gill-rakers on its leading edge and these, in turn, bear small lateral lamellae projecting towards, if not interdigitating with those of the neighbouring outer rakers. Short rakers are present on the distal part of the 1st epibranchial's inner margin, extending to a point level with the uncinate process. There are no gill-rakers on the other epibranchials.

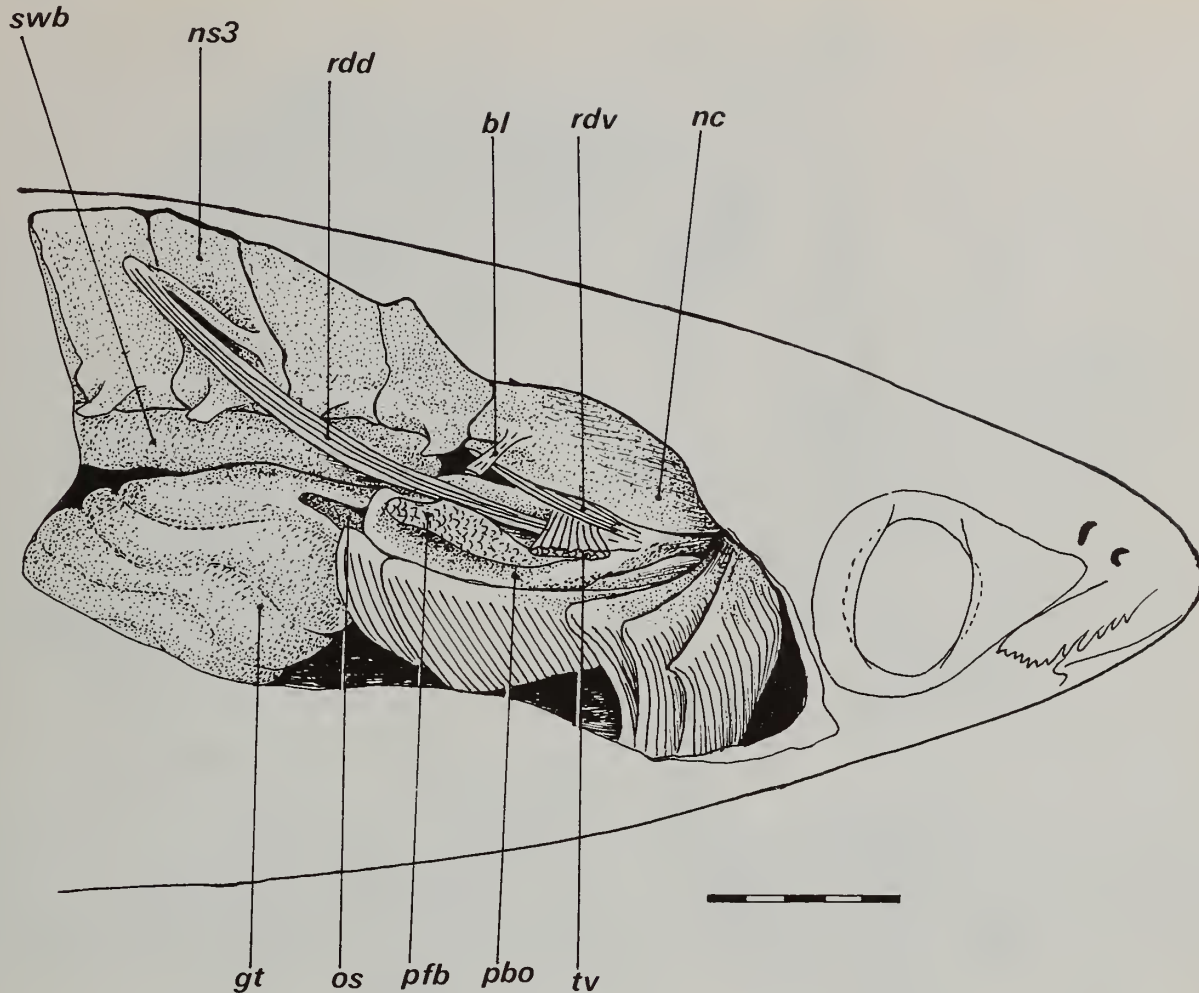The *ceratobranchials* are long; the 1st bears long outer

Fig. 3 *Liza waigiensis* (BMNH 1974.5. 25: 3649–73, 97 mm SL). Dissection of head to show unique configuration of *retractor dorsalis* muscle; the right half of the PBO has been cut away.

gill-rakers similar to those on the 1st epibranchial, and lies well anterior to the denticulate area of the PBO. The 2nd and 3rd ceratobranchials have shorter and closer-set gill-rakers and lie anterior to the PBO, although the posterior rakers of the 3rd surround part of the sulcus border. The 4th cerato-branchial surrounds the lateral face of the denticulate area, and the 5th, which is an expanded lamniform bone, cups the posteromedial region of the organ. The medial border of the 5th ceratobranchial bears proximal-type teeth which are distinct in the juveniles but remain relatively small, if not vestigial, in adults (p. 119). The gill-rakers on the inner surfaces of the ceratobranchials are spaced and orientated in such a way that when drawn together, they intermesh with the outer rakers of the next arch. Since the gill-rakers of the 4th and 5th ceratobranchials enclose the denticulate cushion, they intermesh with the distal teeth of the organ. Several types of gill-raker can be recognised in mugilids (Ingham, 1952). The cartilaginous tips of the 2nd-4th ceratobranchials, which articulate with those on the epibranchials, are drawn out into scytheshaped blades; from these run the rows of gill filaments which pass away from and above the epibranchials and are supported only by their transverse membrane (Fig. 7).

DEVELOPMENT

The following ontogenetic observations apply to *Mugil cephalus*, *Liza saliens*, *L. aurata*, *L. ramada* and *Chelon labrosus* from the Mediterranean.

External morphology: The PBO is at least moderately developed in specimens of *ca*. 11 mm SL. *Liza* spp of this size have folds on the anterior part of the lateral wall which are the precursors of the valves characteristic of adult PBOs and are referred to as *valve precursors* (VP). There is a short-based VP anteroventrally, which is not always distinct, and a long-based VP posteriorly. Both are moderately papillate but neither projects prominently from the wall of the PBO; indeed the posterior VP covers and lies flush within the narrow sulcus. The posterior VP of *Liza* and *Chelon* appears to be homologous with the single long-based VP of *Mugil*. In *Mugil cephalus* of 14.5 mm SL the single fold is distinct and the sulcus is relatively broad, unlike the condition in *Liza* of the same size. In *M. cephalus* above 15 mm SL the transition from VP to adult valve involves little modification, the fold merely becomes proportionately larger and more distinct, particularly in specimens above 20 mm SL. In *Liza* of 15–20 mm SL the VPs also enlarge but the anterior fold remains relatively small and the sulcus narrow (Fig. 8A). In *Chelon* of the same sizes both VPs are large and bulbous and the sulcus is broader (Fig. 8B).

Between 20–34 mm SL the VPs in *Liza* and *Chelon* undergo further changes. The anterior VP becomes more fleshy and prominent but retains its shorter base. In *Chelon labrosus* and *Liza saliens* of *ca*. 33 mm SL the anterior valve has an accessory process, which in *L. saliens* of *ca*. 50 mm SL develops into an elongate flap. The posterior VP becomes distinctly triangular but the transition to its final form varies between taxa. In *C. labrosus* and *Liza aurata* the valve remains long-based, large and fleshy; in *L. ramada* the
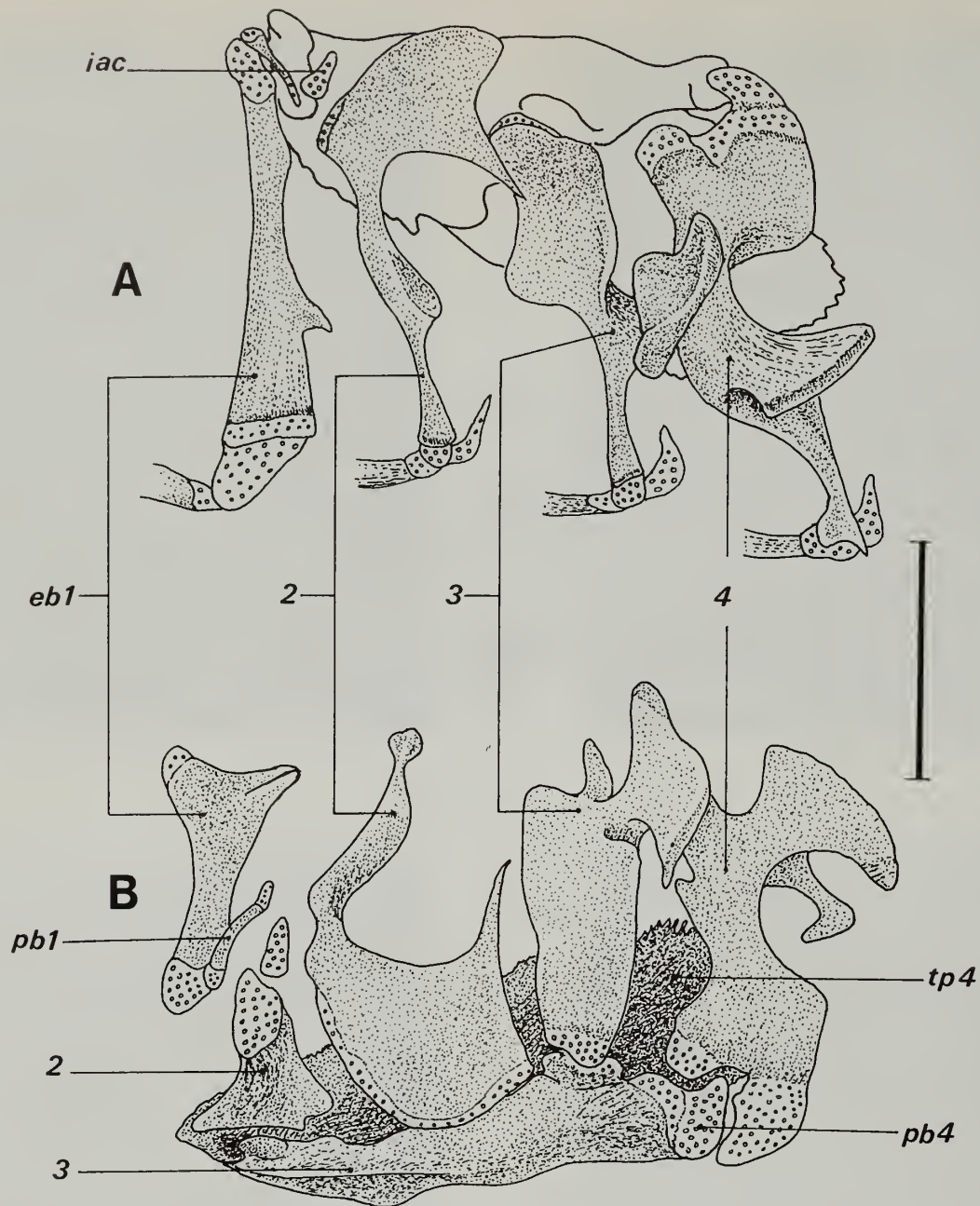
Fig. 4 Upper gill-arch elements of *Mugil cephalus* in A, dorsal and B, medial views. For clarity, in A, the toothplates are shown in outline only. Specimen PA 271186T, 27.5 mm SL. Scale = 0.5 mm.

ultimate structure is a small protruberance, the original long fold remaining as its fleshy base. Between 30–44 mm SL these three taxa also develop a secondary valve or protruberance from the ventral part of the posterior VP. The sulcus is present in the earliest available stages as a narrow and shallow groove. The principal changes in its morphology occur between *ca.* 23–40 mm SL and involve increases in breadth and depth. The most significant development is the opening and widening of the dorsoposterior aperture beneath the 4th epibranchial (Fig. 1A).

Skeletal elements: Discounting intergeneric and interspecific variability in the adult form, the basic ontogeny of the upper gill-arch elements follows the same pattern in all taxa studied. At the earliest available stage (12.5 mm SL *Liza ramada*, Fig. 9A), the toothplates are triangular and meet one another along their respective straight, posterior and anterior borders, The 4th toothplate is shorter than the 3rd and both bear a few proximal-type teeth mostly along their outer margins. Along its posterior border the 3rd pharyngobranchial bears two small cartilaginous processes; a lateral one articulating with the 3rd epibranchial and a medial one articulating with the

cartilaginous 4th pharyngobranchial which, in turn, articulates with the 4th epibranchial. The 2nd pharyngobranchial bears distinct proximal teeth.

In a 14 mm SL *Liza saliens* (Fig. 9B), the situation is similar but the articular processes have extended and a thin laminate keel has developed from the base of the lateral process to extend anteriorly. The base of the 4th epibranchial has expanded to overlap the 4th pharyngobranchial. The teeth are of the proximal type.

At 16–18 mm SL (Fig. 9C), the articular processes of the 3rd pharyngobranchial have developed substantially. A strong keel runs anteriorly from the base of the lateral process whose articular surface has become partially ossified. The anterior border of the 4th pharyngobranchial toothplate has developed a strong lip which abuts the lateral articular process of the 3rd pharyngobranchial. The base of the 4th epibranchial has expanded and nearly reaches the medial articular process of the 3rd pharyngobranchial. Differentiation of the pharyngeal dentition is apparent at these stages; laterally the 4th toothplate bears teeth intermediate in length and thickness between proximal and distal morphotypes. In a 16.5 mm SL *Mugil cephalus*, and at subsequent stages, teeth are absent from the 2nd pharyngobranchial.
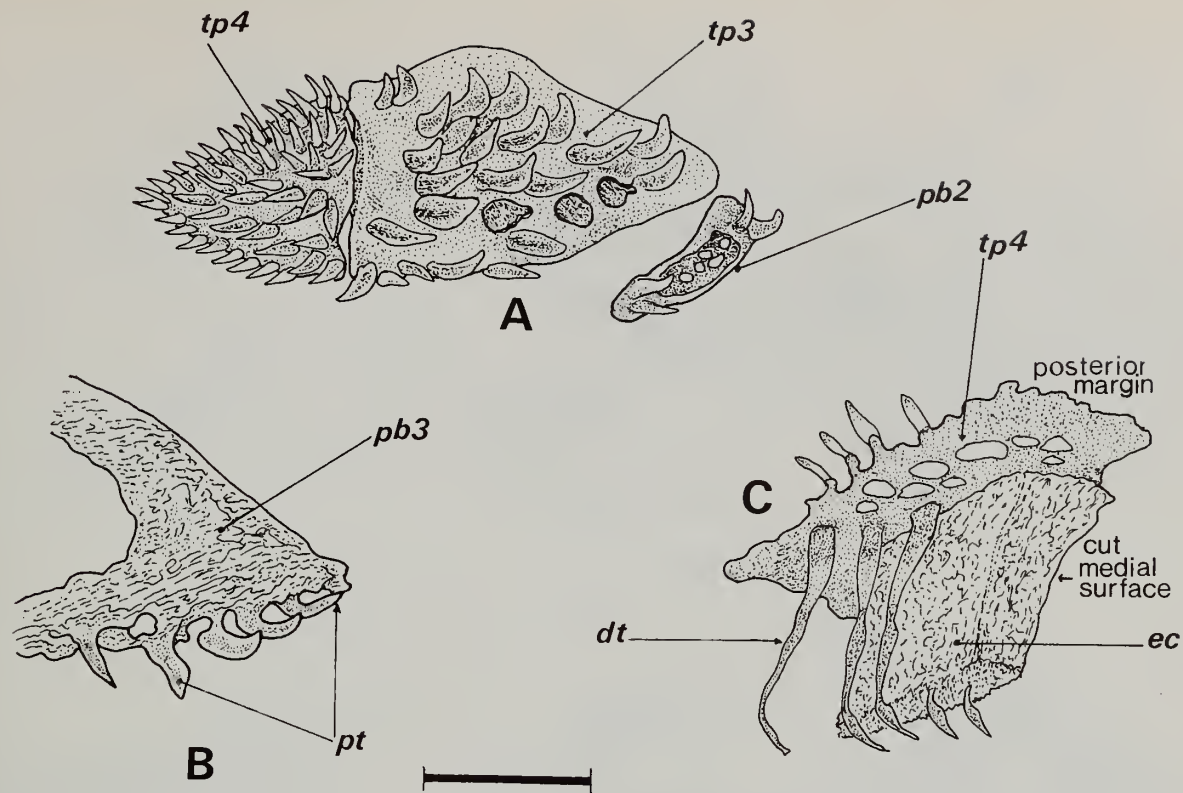
Fig. 5 Pharyngobranchial teeth in A, *Agonostomus* sp. (BMNH 1985.3. 18: 22–37, *ca*. 35 mm SL), ventral view of toothplates, all teeth are of the proximal-type. B & C, *Chaenomugil proboscideus* (BMNH 1903.5. 15: 278–9, 56 mm SL); B shows anterior tip of pharyngobranchial 3 bearing proximal-type teeth; C shows part of a row of distal-type teeth on pharyngobranchial 4 toothplate, the epithelial cushion has been cut away to expose entire shafts of lateral teeth. N.B., teeth stemming from the free lateral margin of the toothplate. B & C viewed ventrolaterally. Scale = 0.5 mm.

At 19–23 mm SL the skeletal elements, including the core of the 1st pharyngobranchial, are well ossified. The dorsal keel of the 3rd pharyngobranchial and the lateral and medial articular processes of both the 3rd pharyngobranchial and 4th toothplate enlarge. The anterior lip of the 4th toothplate elevates to contact the surface of the lateral articular process rising from the 3rd pharyngobranchial. The teeth are characteristically of the distal-type on the lateral part of the 3rd pharyngobranchial toothplate and entirely so on the 4th which expands and lengthens to more than half the length of the 3rd.

At 28 mm SL the 4th toothplate is distinctly broadened and its length usually equals that of the 3rd. Both are covered principally by distal-type teeth although a few proximal-types may remain on their medial borders. At a later stage (36 mm *L. saliens*, Fig. 9D) the adult pharyngobranchial characteristics are developed. The lateral process, articulating with the 3rd epibranchial, is now positioned centrally due to the lateral expansion of the toothplate. The 'lip' of the 4th toothplate border is now a thin lamina adpressed to the lateral and part of the medial processes of the 3rd pharyngobranchial. Later, as the medial process extends further posteriorly, the dorsal lamina of the 4th toothplate makes more extensive contact with it and presumably aids its support. The 2nd pharyngobranchial bears one or two 'intermediate-type' teeth (see above). At *ca*. 30 mm SL and above the 2nd pharyngobranchial is edentulous in all taxa examined.

The 5th ceratobranchial appears slender in the smallest specimens examined and it bears proximal-type teeth. During ontogeny this ceratobranchial expands anterolaterally to oppose the developing 3rd and 4th pharyngobranchial toothplates. The proximal teeth become restricted to a narrow band on the medial border of the 5th ceratobranchial in fish of *ca*. 30 mm SL. At later stages these teeth appear progressively less distinct and eventually vestigial.

POSSIBLE MODE OF FUNCTION OF THE PBO

Information on the function of the PBO is lacking but in previous descriptions of the organ it has been hypothesised to play an important sensory and mechanical role in the sampling and filtration of the water currents laden with food material (Odum, 1968; Capanna *et al*., 1974; Ching, 1977; Drake *et al*., 1984). Having studied the gross and micro-anatomy of the PBO in *Liza ramada*, Capanna *et al*. (1974) arrived at a functional hypothesis which depends on there being a narrow and restricted buccopharyngeal cavity preventing entry of large particles into the gut. They supposed that the denticulate area, nested within the branchial basket, provides the mechanical factor in food particle selection (see below), whereas they assumed that the sulcus (which they termed the 'gustatory region') acts as a chemical sampler.

We agree with the basic functional hypothesis of Capanna *et al*., but surmise that the sulcus plays a more active role as the principle flow channel for the particle-laden water, as well as being a sampling area. The role of the valve(s) is more difficult to determine. Capanna *et al*. (1974) considered them to be sites of mucus production, but disparity in size and shape also suggests a role as water-current controllers. In *Mugil cephalus*, for example, when 'closed' the valve almost occludes the entrance to the sulcus (Fig. 10).

We suggest that the particle-laden water current is initially directed up the sulcus where it is chemically sampled. If found
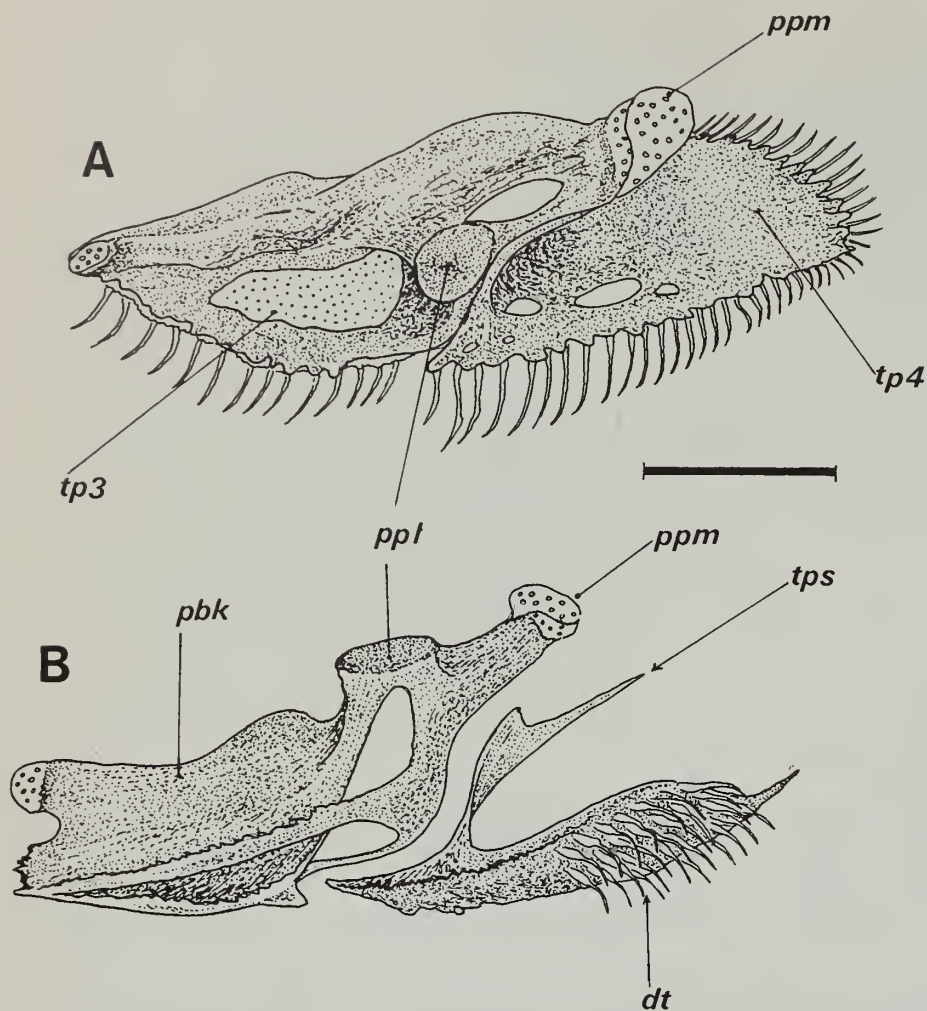
Fig. 6 3rd & 4th pharyngobranchials and tooth-plates of *Mugil cephalus* (PA 271186T, 27.5 mm SL) in A, dorsal and B, lateral views. In B, the 4th toothplate has been separated from the 3rd pharyngobranchial to show detail of opposing surfaces. For clarity, the 3rd toothplate has been removed from its supporting bone and only a few distal teeth are shown on toothplate 4. Scale = 0.5 mm.
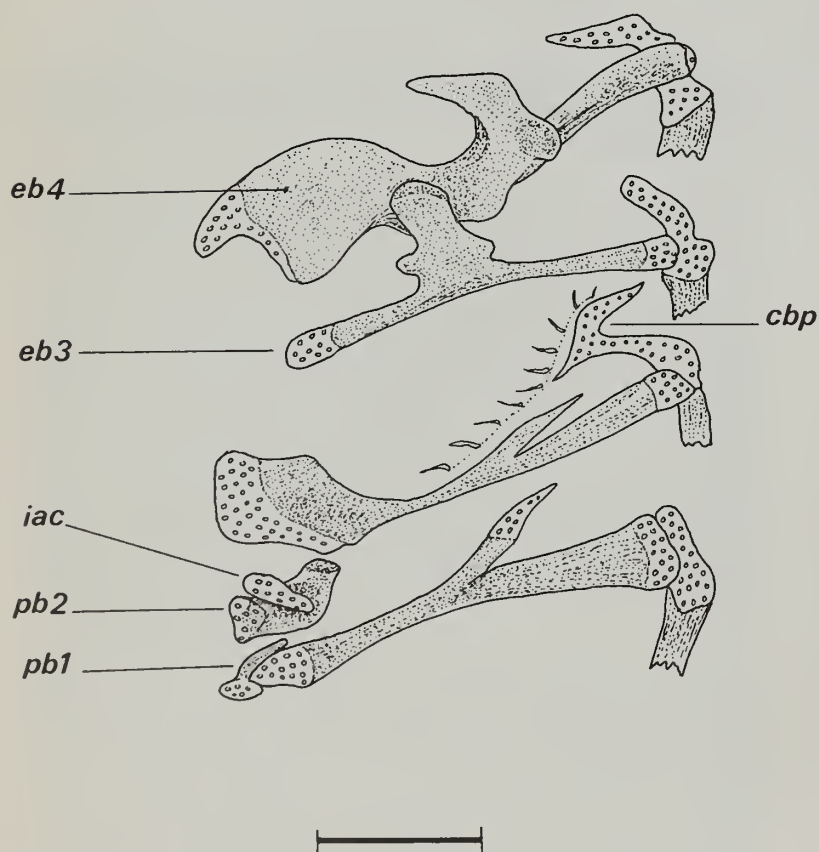
Fig. 7 Upper gill-arch elements of *Liza ramada* (PA 17986T, 57.5 mm SL). Gill-filaments are shown extending from the 2nd cerato-branchial process to above the uncinate process of the 2nd epibranchial. Scale = 0.5 mm.

suitable for filtering the current is then forced over the sulcus border and filtered across the denticulate area. Small corruga-tions along the border possibly aid in channelling and altering the nature of the flow of the current as it is ejected from the sulcus. The mechanism of ejection is most likely achieved through elevation of the pharyngobranchial unit by the *levator internus* 2, an action which might also displace the anterior fat body outwards, thus sealing the sulcus dorsally.

According to Capanna *et al.* (1974) the particle-laden current passes between the denticulate area and the intermeshing rakers which prevent the passage of coarser material. The structure of the PBO indicates to us that it may be able to regulate its filtering capacity by adjusting the degree of separation between the denticulate area distal-type teeth and the gill-rakers. The larger distal-type teeth along the sulcus margin and lateral face of the denticulate area presumably serve to entrap the coarser material as do the anteromedial proximal-type teeth. Transport of the particulate matter to the oesophagus is possibly *via* streams of mucus emmanating from the valve area (Capanna *et al.*, 1974), Ojha & Mishra, (1987), report mucous gland openings at the base of the gill-rakers in *Rhinomugil*). Observations (eg., Günther, 1861; Hickling, 1970) indicate that sediment is worked for some time between the pharyngeal bones, implying that material is passed over the denticulate area more than once by a circulating current. Such a current would carry the mucus posteriorly to meet the filtrate behind the PBO (Fig. 11). It is noted that the oesophageal opening is not in the same horizontal plane as the buccal cavity but elevated to just beneath the vertebral column (Fig. 3).

According to *in vivo* observations of Capanna *et al.* (1974), the non-ingested particles are removed from the PBO by
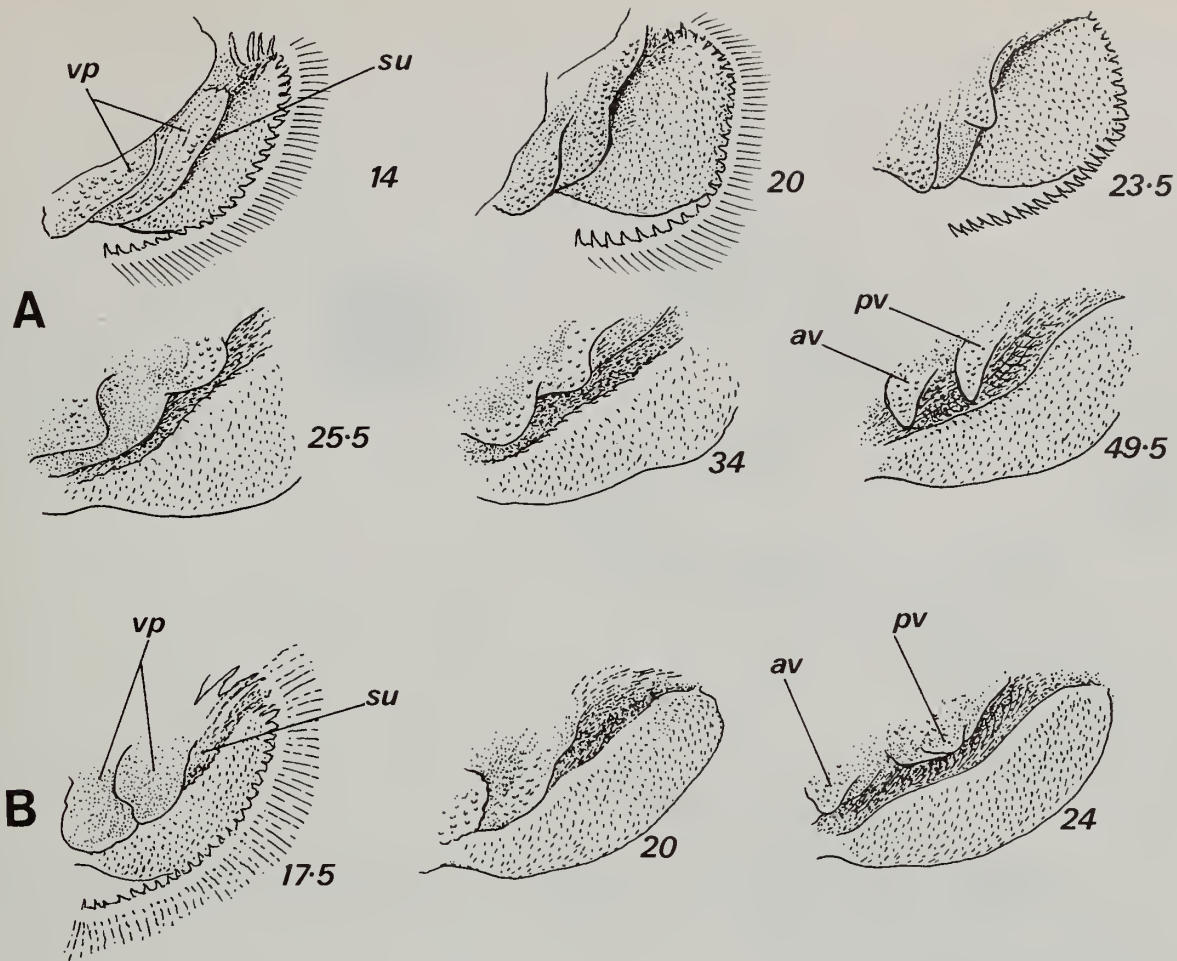
Fig. 8 Developmental series of the PBO in A, *Liza saliens* (PA 17986R) and B, *Chelon labrosus* (PA 19685R). First three figures in ventrolateral view, others lateral. Numbers indicate SL (mm).

'vibratory release movements imparted by the intrinsic muscles of the organ's denticulated valve' (*ie.*, *levator internus* 2 muscle). In this way the denticulated area is possibly agitated against the gill arch which would rake the mulch of particles off its surface. Any strands of detritus (*eg.*, filamentous algae) which became attached to the gill-rakers might be removed by the rakers of neighbouring ceratobranchials when these are drawn together and their rakers intermeshed (see above). In this way the gill-rakers' own close intermeshing might act as a self-cleaning mechanism. The noningested material is flushed out of the mouth (Günther, 1861; Hickling, 1970; Capanna *et al.*, 1974). The sulcus and its ventral valve may well contribute to the flushing process by directing the flow when the buccal cavity is evacuated.

The hypothesis that the sulcus, valves and denticulate area play important roles in the sampling and filtration of the water current passing over them is supported by simultaneous morphological and trophic changes during ontogeny. There is a certain amount of interspecific variability in diet as well as that related to locality and habitat (see below). Nonetheless, there is a consistent trend for mugilids to show a trophic shift from exclusive carnivory (taking neustonic zooplankton during postlarval stages) to ilyophagy in juvenile and adult stages (Ebeling, 1957; Thomson, 1966; Ching, 1977; also De Silva, 1980 and Brusle, 1981 for literature reviews).

Mugilids usually assume the adult diet prior to 50 mm SL. Most previous work indicates that the principal dietary phase transition in fish occurs between 20–30 mm SL (Ebeling, 1957; Hickling, 1970; Albertini-Berhaut, 1973, 1974; Ching, 1977; De Silva & Wijeyaratne, 1977; Ceccherelli *et al.*, 1981; Ferrari & Chieregato, 1981; Tosi & Torricelli, 1989). Work

by Blaber & Whitfield (1977) and Chan & Chua (1979) suggests that the dietary transition may even occur in fish of between 10–20 mm SL. The simple structure of the PBO during postlarval stages and the predominance of proximal-, rather than distal-type teeth both on the denticulate area and 5th ceratobranchial suggest the fish are better suited for the selection of planktonic items.

A functional hypothesis of the PBO should take into account mouth and buccal cavity morphology and movements. Such studies are beyond the scope of this survey but it may be mentioned that jaw and pharyngeal pouch teeth have a similar morphology and ontogeny. The upper and lower jaw teeth form from a thin lateral margin of bone (staining only with alcian blue at all growth stages), which becomes foraminated, fretted, and eventually shredded into the strands which form the tooth-shafts. Furthermore, there appears to be some correlation between lower jaw shape (ventral profile) and PBO morphotype (Fig. 19F). Marais (1980) and Drake *et al.* (1984) concluded that jaw tooth morphology is an important factor in determining diet. We note that the 'fringes' of jaw teeth in such forms as *Chaenomugil* and *Neomyxus* (Fig. 19A & B) possibly play a role in pre-oral selection.

TAXONOMIC SURVEY OF PBO

AGONOSTOMUS Bennett, 1832 (Fig. 12A): PBO absent; pharyngobranchial 3 orientated horizontally, with 2nd, and
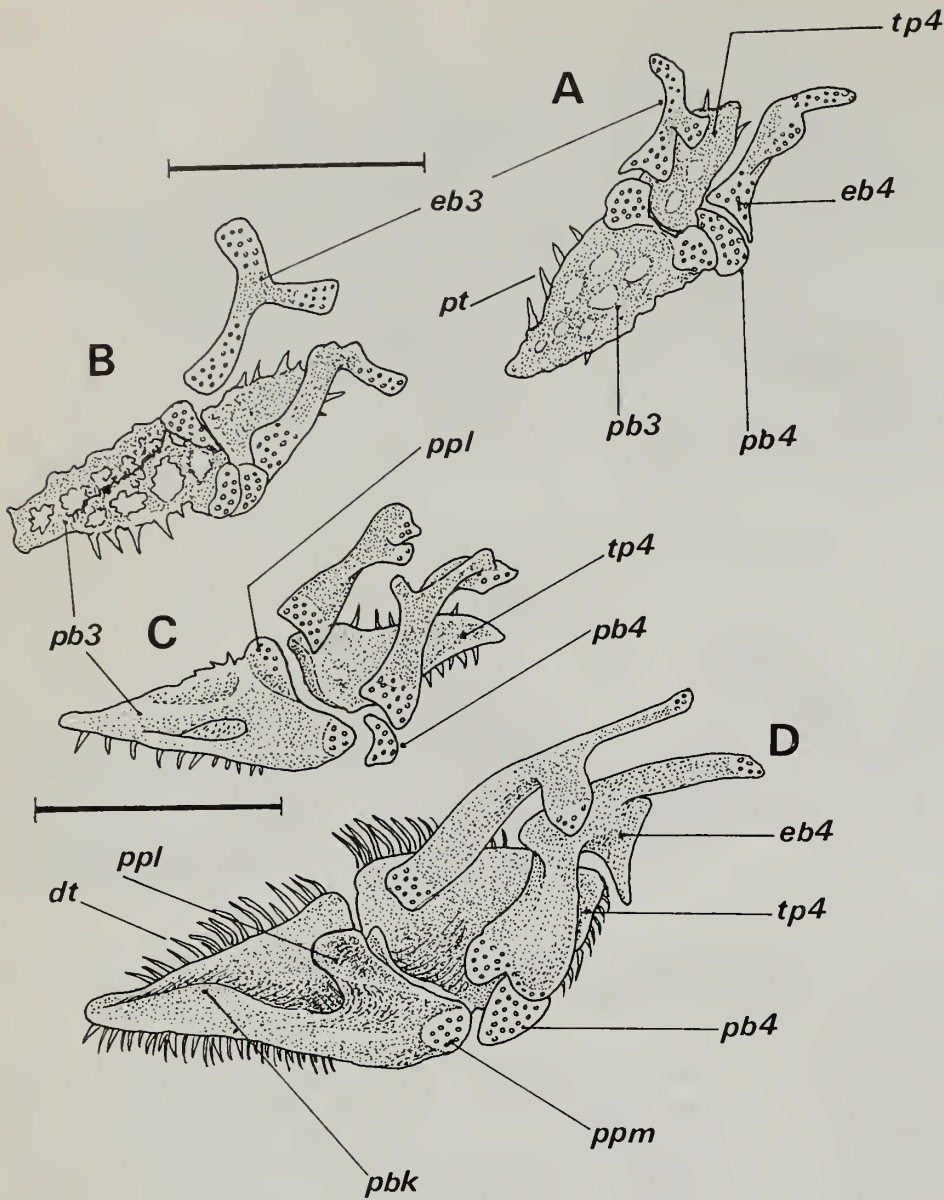
Fig. 9   Developmental series of right pharyngo-branchials and 3rd and 4th epibranchials in A, *Liza ramada* of 12.5 mm SL (PA 17986R), B-D, *Liza saliens* of 14, 18 (PA17986R) and 36 mm SL (PA281086R). A and B in dorsal, C and D in dorsolateral views. Scales = 1 mm.
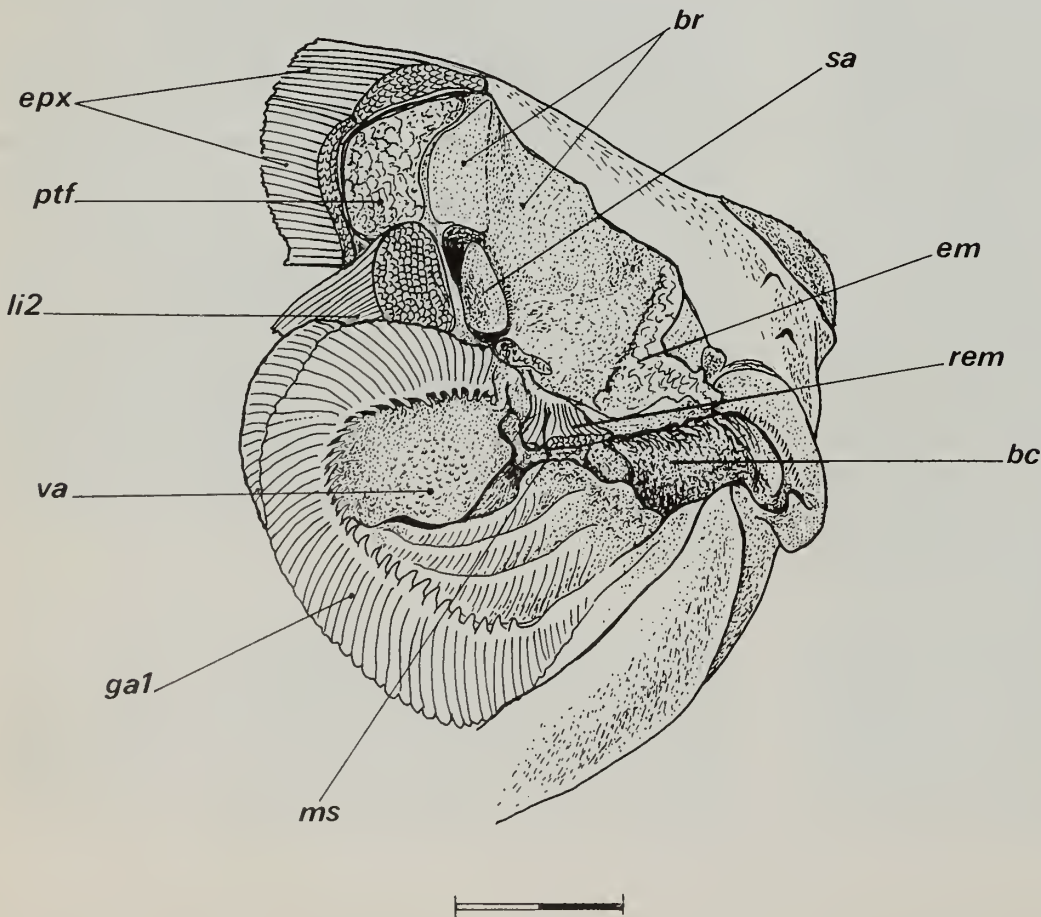
Fig. 10   *Mugil cephalus* (PA 13386T, 48 mm SL). Oblique frontal view of dissected head showing buccal cavity and position of sulcal valve; the rakers of the 1st gill-arch crossing the valve have been cut, normally they extend across the front of it. Other features shown are muscles and fat bodies lying within the cranium.
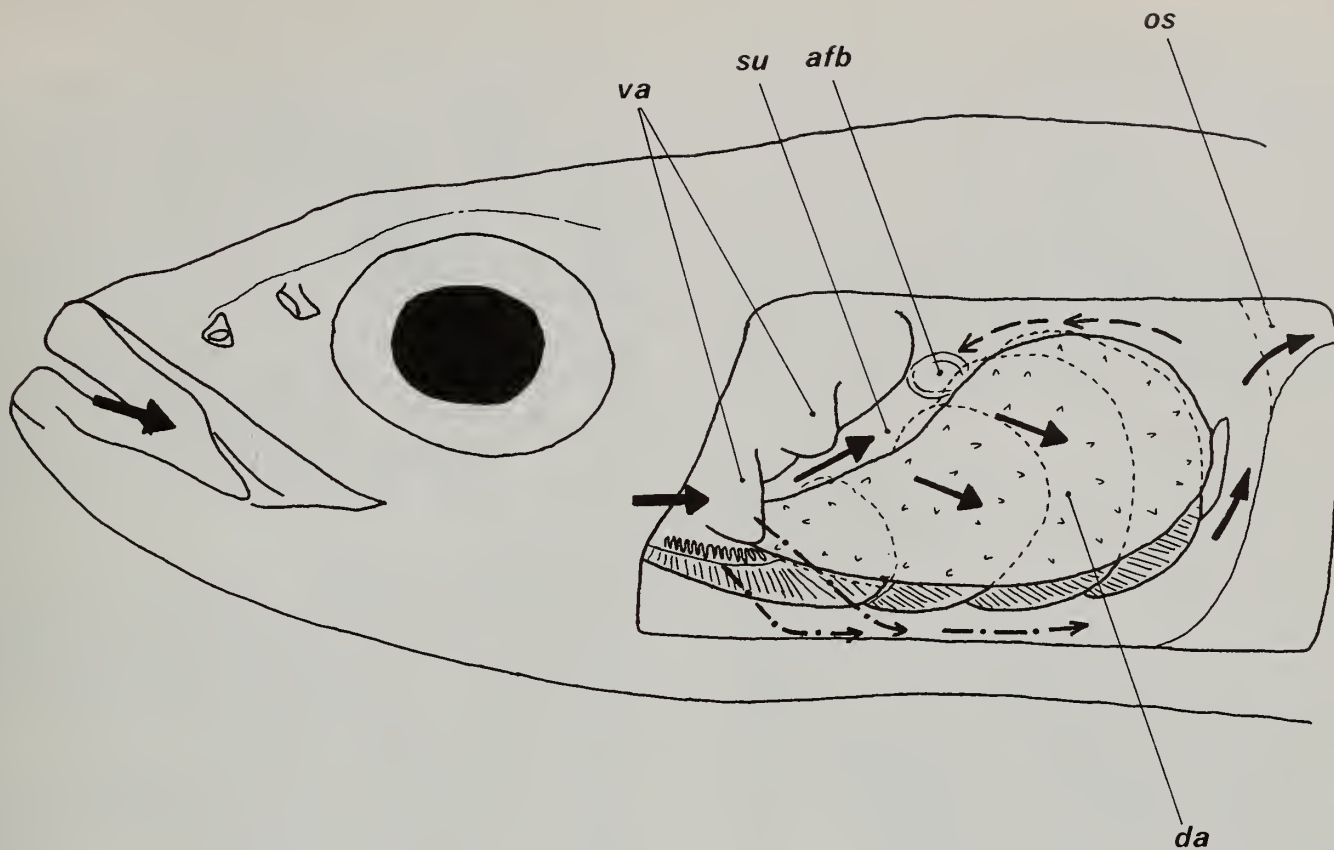
Fig. 11 Diagrammatic representation of hypothesised flow of food-laden water (thick arrow), filtered and recirculated water (dashed arrow), and mucus (dashed/dotted arrow) around PBO. The surrounding gill-arches are indicated by broken lines.
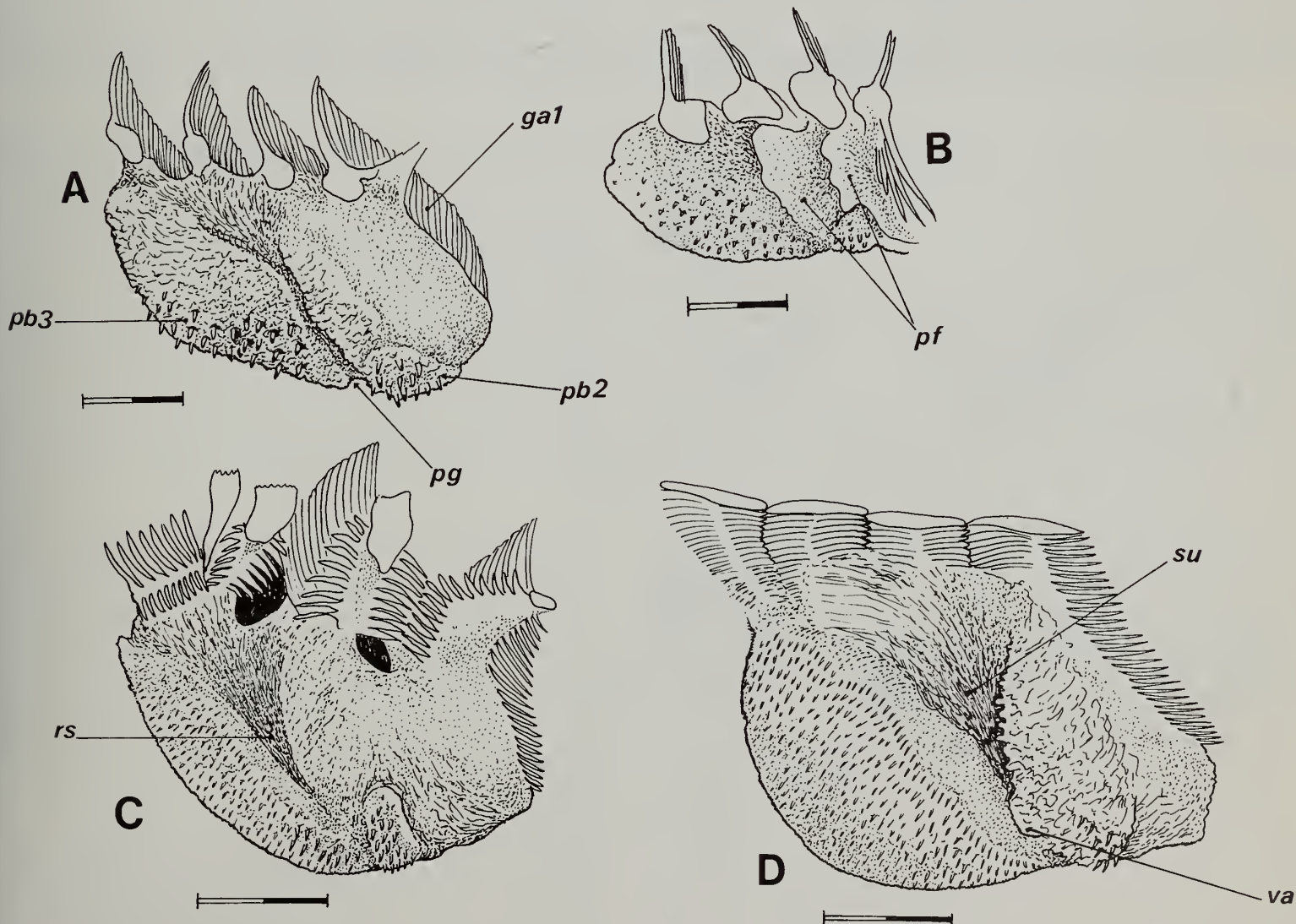

Fig. 12 PBO of A, *Agonostomus monticola* (BMNH 1985.3.18: 139–141, 127 mm SL); B, *Joturus pichardi* (1933.3.6: 199–204, 113 mm SL); C, *Cestraeus oxyrynchus* (1879.3.4: 1, 108mm SL); D, *Aldrichetta forsteri* (1899.2.14: 38–43, 178 mm SL). All in ventrolateral view of right side.

3rd and 4th toothplates bearing strong, downwardly pointing (proximal) teeth (Fig. 5A). Thick epidermal tissue surrounds toothplates and proximal portions of epibranchials, forming 'pharyngeal pads' which are widely separated across the midline. Condition similar in both species examined, *A. telfairii, A. monticola*.

JOTURUS Poey, 1860 (Fig. 12B): PBO absent; upper pharyngeal morphology similar to that of *Agonostomus* but with two loose folds of tissue covering the area between the 2nd and 3rd pharyngobranchials. When the fold covering the anterior border of toothplate 3 is lifted, a rudimentary sulcus is exposed.

CESTRAEUS Valenciennes, 1836 (Fig. 12C): PBO rudimentary; pharyngeal morphology similar to that of *Joturus* but lacking folded tissue; although a rudimentary sulcus is present, that of *C. oxyrynchus* and *C. plicatilis* (type species) is deeper and more well-defined than that of *C. goeldii*.

ALDRICHETTA Whitley, 1945 (Fig. 12D): PBO morphology intermediate between *Cestraeus* and more advanced mugilids; sulcus V-shaped, narrow and shallow. Teeth on pharyngobranchial 2 and medial teeth on 3, of proximal-type, outer teeth and all those on 4th toothplate are of distal-type. Tissue anterior to sulcus highly convoluted and papillose, covering a medial fat body between 2nd and 3rd epibranchials. Pharyngobranchial pads broadly separated by deep furrow.

MYXUS Günther, 1861 (Fig. 13A): PBO developed; denticulate area large with broadly convex sulcus border; cushions deeply divided; sulcus wide, diagonal; valve in form of a double papillose pad. Of the included species, *M. elongatus* (type species) and *M. petardi* closely resemble one another

but *M. capensis* has a PBO morphology which more closely resembles that of *Mugil cephalus* (p. 125).

SICAMUGIL Fowler, 1939 (Fig. 13B): PBO with shallow denticulate area, sulcus border almost straight; sulcus diagonal, wide and shallow; single large valve situated anteroventrally, its anterior border infolded forming a pocket. Denticulate cushions widely separated by a ridge which expands anteriorly into a conical structure lying between the lateral valve-pockets.

RHINOMUGIL Gill, 1863 (Fig. 15D): PBO with moderate denticulate area, straight sulcus border bearing a row of prominent papillae; sulcus diagonal, rather broad, a well-developed valve at lower end which has a papillate inner surface. Teeth are exceptionally fine and hidden in mucosa; those along the sulcal margin only slightly enlarged, as are the proximal teeth.

NEOMYXUS Steindachner, 1878 (Fig. 14A): PBO with extensive denticulate area; teeth arranged in transverse rows, those along sulcus border and over dorsoanterior area setiform; cushions widely separated posteriorly, a transverse papillose septum anteriorly; sulcus deep, vertical and narrow, with a tripartite valve at lower end.

CHAENOMUGIL Gill, 1863 (Fig. 14B): PBO with reduced denticulate area; cushions deeply divided, teeth arranged in regular rows, those along sulcus border setiform; sulcus border markedly concave; sulcus extensive, no valves.

CHELON Röse, 1793 (Fig. 14C): PBO with denticulate area relatively large, cushions deeply divided, posterolateral distal-type teeth of almost even size, those anteroventrally longer and anteriorly curved; sulcus border slightly corrugated
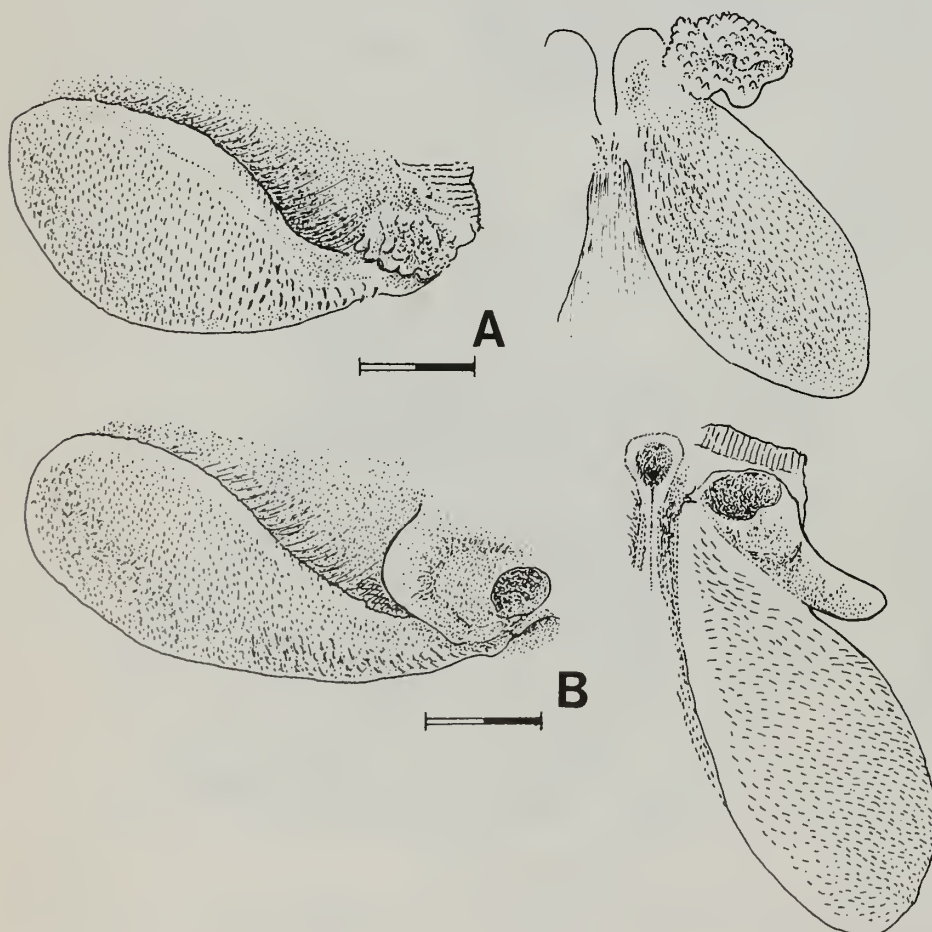

Fig. 13 PBO of A, *Myxus petardi* (BMNH 1914.8.20: 258–61, 118 mm SL); B, *Sicamugil hamiltoni* (1891.11.30: 80–81, 105 mm SL), in lateral and ventral views of right side.
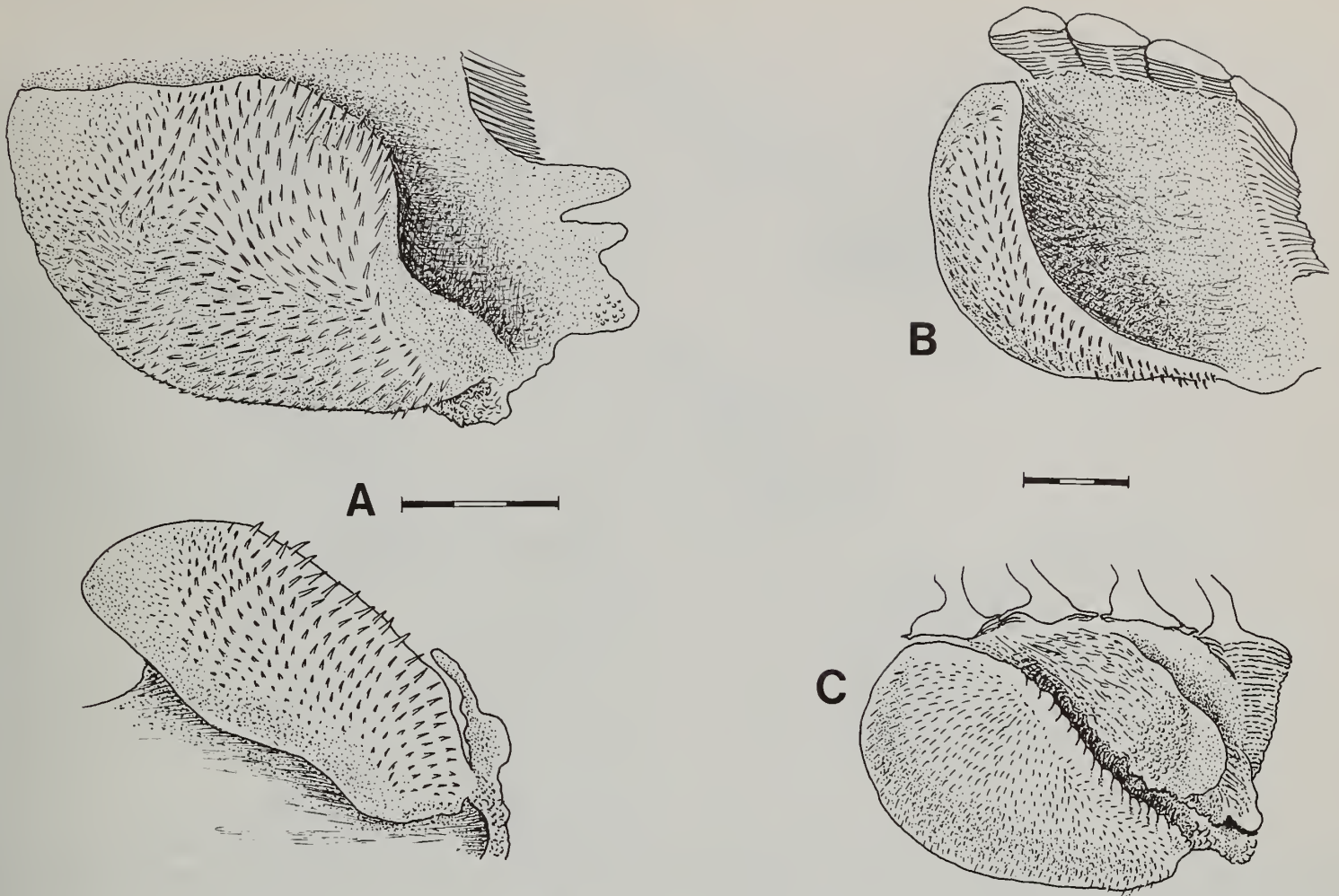
Fig. 14 PBO of A, *Neomyxus leuciscus* (BMNH 1877.7.24: 13, 200 mm SL), in lateral and ventral views (valve open forward); B, *Chaenomugil proboscideus* (1908.5.15: 278–9, 185 mm SL); C, *Chelon labrosus* (1962.7.30: 746, 107 mm SL). Lateral views of right side.

ventrally; sulcus diagonal and narrow, with a large fleshy, papillate valve and smaller ventral valve at lower end.

OEDALECHILUS Fowler, 1903 (Fig. 15): PBO with relatively small denticulate area, cushions widely separated, distal teeth evenly graded; sulcus diagonal, narrow, with fleshy valve and ventral finger-like process at lower end. This description applies to the type species, *O. labeo*, but in *O. labiosus*, the denticulate area is large, with abruptly graded distal-type teeth, those on the sulcus border being larger while those anterolaterally are posteriorly curved; sulcus border slightly concave, elevated dorsoposteriorly; sulcus nearly vertical, wide and with single large valve at lower end (Fig. 15B).

MUGIL Linnaeus, 1758 (Figs 16 & 17): In the type species, *Mugil cephalus*, from the Mediterranean, the PBO has a large denticulate area with finely size-graded teeth, those along the sulcus border being the largest; sulcus wide, near vertical, with a single large valve at lower end. In *M. cephalus* from other geographical areas there are marked differences in the sulcus and in valve size. Indeed, there seems as much intra- as interspecific variability in the organ, which casts doubt on the specific integrity of *M. cephalus*. Species with a PBO morphology similar to that in *M. cephalus s.s.* are *M. bananensis* (with finer teeth; Fig. 16F), *M. curema*, *M. trichodon* and *M. incilis* (Fig. 16G). In *M. capurii* the denticulate area is larger and bears longer, setiform teeth; the sulcus valve is triangular. *Mugil liza* has only a moderate denticulate area and a diagonal sulcus with small valve (*cf. M. cephalus* of Indian Ocean, Fig. 16A), features in which it more closely resembles

some *Liza* species (see below). *Mugil hospes* has further differences; the denticulate area is extensive, being half the length of the entire PBO; the sulcus is nearly vertical, with a highly papillose valve (Fig. 17A). *Mugil thoburni* and *M. setosus* also differ from other *Mugil* in having a reduced denticulate area with greatly enlarged teeth along the sulcus border, and an extensive, vertical sulcus with a valve so large that it completely covers the sulcus' lower end (Fig. 17B).

CRENIMUGIL Schultz, 1946 (Fig. 15C): The description is of the condition in the type species, *C. crenilabis* (see below, p. 130). PBO with moderate denticulate area, teeth along sulcus margin setiform, in two rows; sulcus extensive, nearly vertical, its wall strongly papillate, especially that area overlying the central fat body; no valve at lower end, but a small fleshy nodule is present ventromedially.

LIZA Jordan & Swain, 1884 (Fig. 18): In one group of species the PBO has a moderately developed denticulate area with fine, almost evenly sized teeth; denticulate cushions deeply but narrowly separated; sulcus margin crenulated; sulcus diagonal and wide with two small valves (whose sizes are interspecifically variable) at lower end, the ventral one papillate. Species with this morphology are *L. aurata*, *L. buchanani*, *L. carinatus*, *L. curvidens*, *L. klunzingeri*, *L. macrolepis*, *L. saliens*, *L. ramada* (type species; Fig. 18A), *L. richardsonii*, *L. trichodon*. Species having a similar overall PBO morphology but lacking valves are *L. dumerilii*, *L. engeli*, *L. falcipinnis*, *L. haematocheilus*, *L. heterochilus*, *L. parvidens*, *L. parsia*, and *L. subviridis*. In *Liza haemato-*
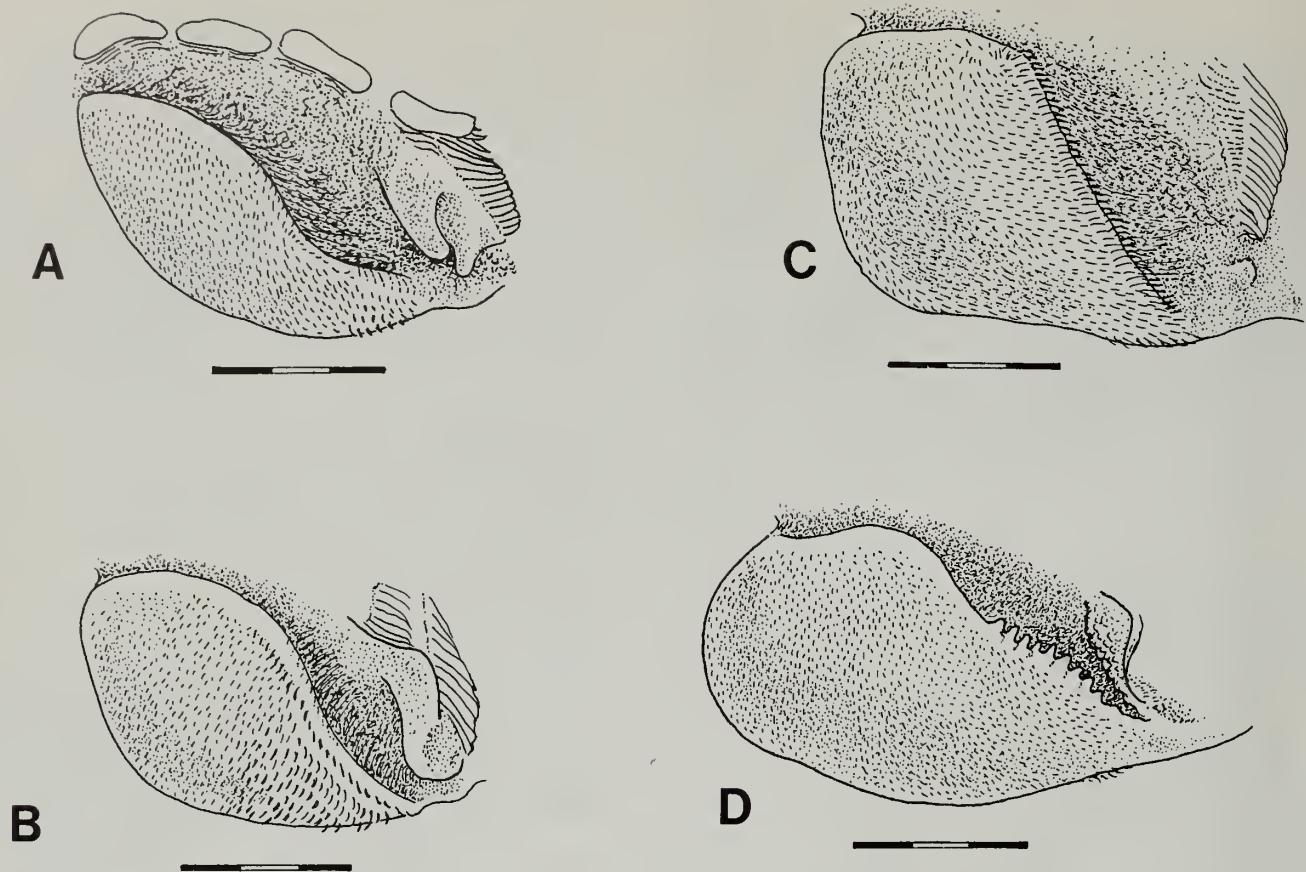
Fig. 15   PBO of A, *Oedalechilus labeo* (BMNH 1948.11.8: 1–10, 148.5 mm SL); B, *Oedalechilus labiosus* (1960.3.15: 1709–15, 83 mm SL); C, *Crenimugil crenilabis* (1951.11.16: 623–30, 107 mm SL); D, *Rhinomugil corsula* (1891.11.30: 89–98, 173.5 mm SL). Lateral views of right side.

cheilus, the sulcus is more extensive than in any other *Liza* and possibly mugilid species (Fig. 18B).

Liza abu more closely resembles *Mugil* in having both a large, lateral denticulate area and a large, single valve (Fig. 18E).

A third group of species with the denticulate area reduced, the teeth fine and evenly graded and the sulcus diagonal and wide, includes: *L. grandisquamis* (Fig. 18D), *L. parmatus*, *L. seheli* and *L. waigiensis* (Fig. 18C).

DISCUSSION

Agonostomus is the most plesiomorphic mugilid in terms of its PBO structure since it lacks the more developed organ of other taxa. The pharyngobranchial teeth are directly attached to the 2nd and 3rd pharyngobranchials and 4th toothplate; the *levator internus* 2 is narrow and the *retractor dorsalis* is a single (paired) muscle. These characters all seem to represent the least specialised condition seen in the Mugilidae. Schultz (1946) distinguished *Agonostomus* from other mugilids on the basis of what are plesiomorphic features *ie.*, broad band of teeth attached to jaw, lack of marginal teeth, absence of lip folds, broadly rounded lower jaw, long maxilla and absence of adipose eyefold tissue.

In constructing a phylogeny for the Mugilidae (Fig. 20) our polarity assignments for PBO morphotypes are based on the premises that *Agonostomus* represents the plesiomorphic lineage (on characters other than the absence of a PBO; see above) and that during ontogeny the more general precedes the less general condition (Løvtrup, 1978; Nelson, 1978;

Fink, 1982). The latter sequence is evident in the possession of proximal-type pharyngobrancial teeth in the earliest stages of all mugilids which are later replaced by distal-type teeth in the majority of taxa (see 'Development'). Our hypothesis thus postulates that the more derived mugilid lineages are those in which distal-type teeth predominate. Those taxa which possess a greater variety of distal teeth morphotypes possibly represent advanced conditions, but more detailed investigations on dental variability are required to evaluate this suggestion.

Joturus is more advanced than *Agonostomus* in having a rudimentary sulcus between the pharyngobranchial toothplates, and in the development of a small, fat-body between epibranchials 2 and 3 (node 1 on Fig. 20); as in *Agonostomus*, there is a narrow *levator internus* and a single *retractor dorsalis*. *Cestraeus* also has a rudimentary sulcus with much-folded and papillose tissue covering a medial fat-body. Proximal-type teeth are present on pharyngobranchials 2 and 3 but the majority on the latter and those on toothplate 4 are of the distal-type. The *levator internus* 2 is somewhat larger than in the other two genera and the *retractor dorsalis* has some anterior fibres attached to the basioccipital (node 2 on Fig. 20). Schultz (1946) considered *Cestraeus* to be the most specialised of a group also including *Xenomugil*, *Chaenomugil* and *Neomyxus*, but there is no evidence from PBO morphology to support this relationship (see also p. 128). *Aldrichetta* has a PBO morphology 'intermediate' between those of the *Agonostomus*—*Cestraeus* series (Fig. 20) and those of other mugilids (see below). Like the *Agonostomus*—*Cestraeus* series, *Aldrichetta* exhibits some teeth on pharyngobranchial 3 which are of the proximal-type and there is a single *retractor dorsalis* although, as in *Cestraeus*, some anterior fibres attach to the basioccipital. In common with
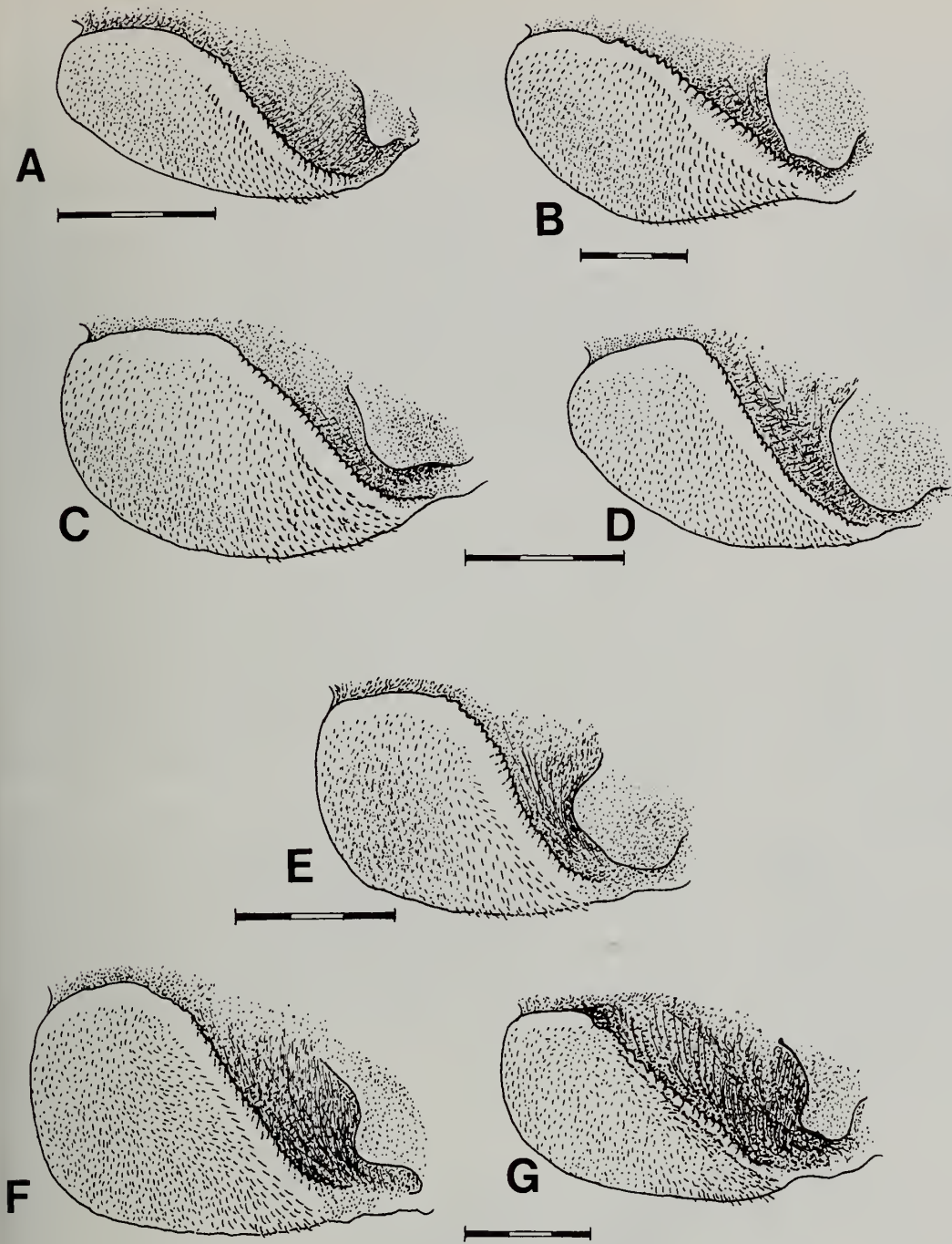
Fig. 16 PBO of *Mugil cephalus* from A, Socotra, Arabian Sea (BMNH 1957.4.24: 98–100, 81 mm SL); B, Kebir River, Latakia, Syria (1968.12.13: 462–4, 125 mm SL); C, Pacasmayo, Peru (1913.7.10: 41–4, 92.5 mm SL); D, Wakenoura, Japan (1923.2.26: 249–53, 73 mm SL); E, Kowie River, South Africa (1975.8.15: 204–212, 87.5 mm SL); F, *Mugil bananensis* (1968.11.15: 91–4, 120 mm SL); G, *M. incilis* (1933.8.2: 70–72, 117 mm SL). Lateral views of right side.

other mugilids there is a well-developed sulcus covering a medial fat-body (node 3 on Fig. 20), and a broad, thick *levator internus* 2.

There seems little doubt that on the basis of PBO morphology *Agonostomus*, *Joturus*, *Cestraeus* and *Aldrichetta* are distinct genera which represent successively advanced lineages (Fig. 20). *Aldrichetta* displays attributes of more advanced mugilids in its development of a sulcus and in having nearly all distal-type pharyngobranchial teeth. The presence of a fat-body and well-developed sulcus indicates a more advanced PBO.

The division of the *retractor dorsalis* into dorsal and ventral segments (dorsal and ventral referring to their insertions with respect to the *transversus* muscles rather than their origins which are both on the vertebral axis) together with the almost complete loss of fully mineralised and ankylosed (proximal-type) pharyngobranchial teeth and development of a sulcus and valves, characterises an advanced assemblage of mugilids which includes the more speciose genera. These genera constitute the two terminal subgroups of the cladogram (*ie.*, groups above nodes 4 and 5 on Fig. 20). It is these genera whose limits remain problematical. Schultz (1946) experienced 'great difficulty in arranging the species of Mugilidae into

genera of concise and of clear definition, owing mostly to the paucity of useful taxonomic characters'. We believe that the PBO morphology is a character-complex that can aid in diagnosing groups.

Those genera which either lack a PBO or possess a rudimentary one (*Agonostomus*, *Cestraeus*, *Joturus*, *Aldrichetta*), have teeth on the 2nd pharyngobranchial and horizontally aligned 3rd and 4th pharyngobranchial toothplates, the condition which is present in early developmental stages of those taxa with a more advanced PBO. Thus, among the advanced assemblage of mugilids (*ie.*, those genera above node 4 on Fig. 20; see discussion above), an increased 4th toothplate area having its lateral surface more vertically orientated is taken to be a derived condition (node 5 on Fig. 20). Included in this group are *Myxus*, *Neomyxus*, *Chelon*, *Oedalechilus labiosus*, most *Mugil* spp, and *Xenomugil*. The plesiomorphic condition, where the 4th toothplate lies nearly horizontally exposing a relatively small, convex lateral denticulate area, is present in *Sicamugil*, *Rhinomugil*, *Chaenomugil*, *Oedalechilus labeo*, *Crenimugil*, and most *Liza* spp. The size of the denticulate area is often negatively correlated with that of the sulcus, since generally the more extensive the
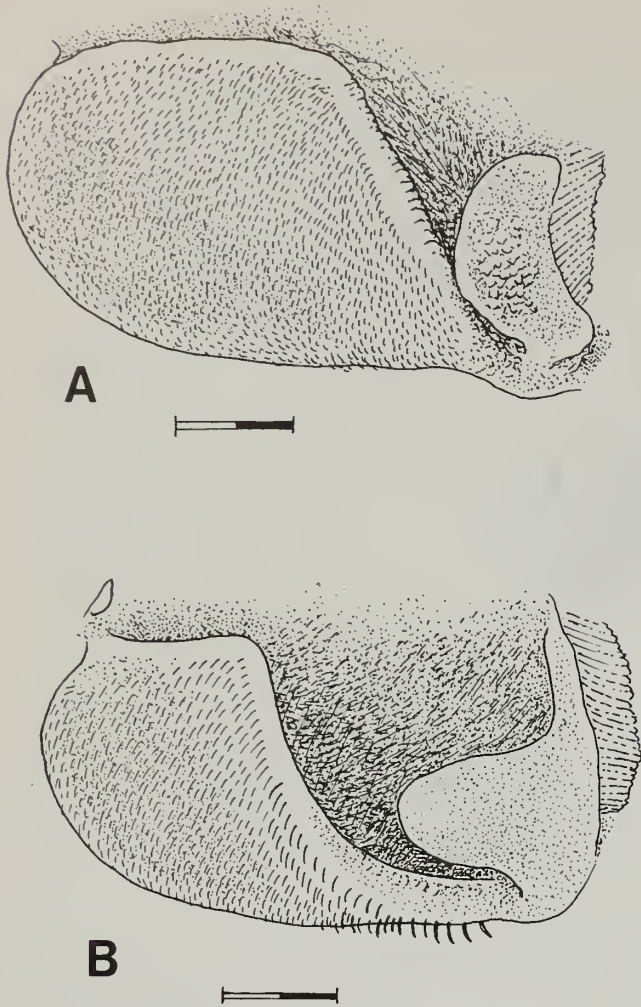
former, the narrower the latter (*eg.*, *Mugil hospes*, *Neomyxus leuciscus*). An extensive sulcus may not, however, indicate the plesiomorphic state since in those taxa with wide sulci (eg. *Liza haematocheilus*) the length of the entire PBO is increased due to the increased distance between the 2nd and 3rd epibranchials.

Considering first the genera exhibiting the more derived condition (*ie.*, those above node 5 on Fig. 20), *Myxus* has a PBO morphology similar to that of some *Mugil* species, but differs from these and other mugilids in its convex denticulate sulcus border. We follow Ingham (1952) in including *Trachystoma petardi* in the genus since its PBO morphotype and jaw dentition are nearly identical to those of the type species *M. elongatus*. Schultz (1946) included in *Trachystoma*, *Mugil capensis* Cuv. & Val., 1836 (= *M. euronotus* A. Smith, as given in Schultz). However, *Mugil capensis* is unlike the other two species in both the form of its PBO and its jaws, the former resembling more closely that of *Mugil cephalus*, the latter those of *Mugil curvidens*.

Neomyxus shares PBO characters (extensive denticulate area, vertical and narrow sulcus) with *Mugil hospes*. Thought by Schultz (1946) and Ingham (1952) to be closely related to *Chaenomugil*, it differs considerably from this taxon in PBO morphology (see p. 124) and lower jaw shape. Although the lower lip of *Chaenomugil* is dependent as in *Neomyxus*, the labial teeth are bicuspid, short, and somewhat posteriorly directed.

Chelon has a similar PBO morphology to some *Liza* species in possessing two valves, but the upper of these is highly papillose (*cf.* the lower in *Liza*). Schultz (1946) unjustifiably synonymised *Liza* and *Oedalechilus* with *Chelon*; *Oedalechilus*, as represented by the type species *Mugil labeo* Cuvier, was thought by Schultz to represent 'the most extreme development of the mouth of *Chelon*'. Trewavas & Ingham (1972)
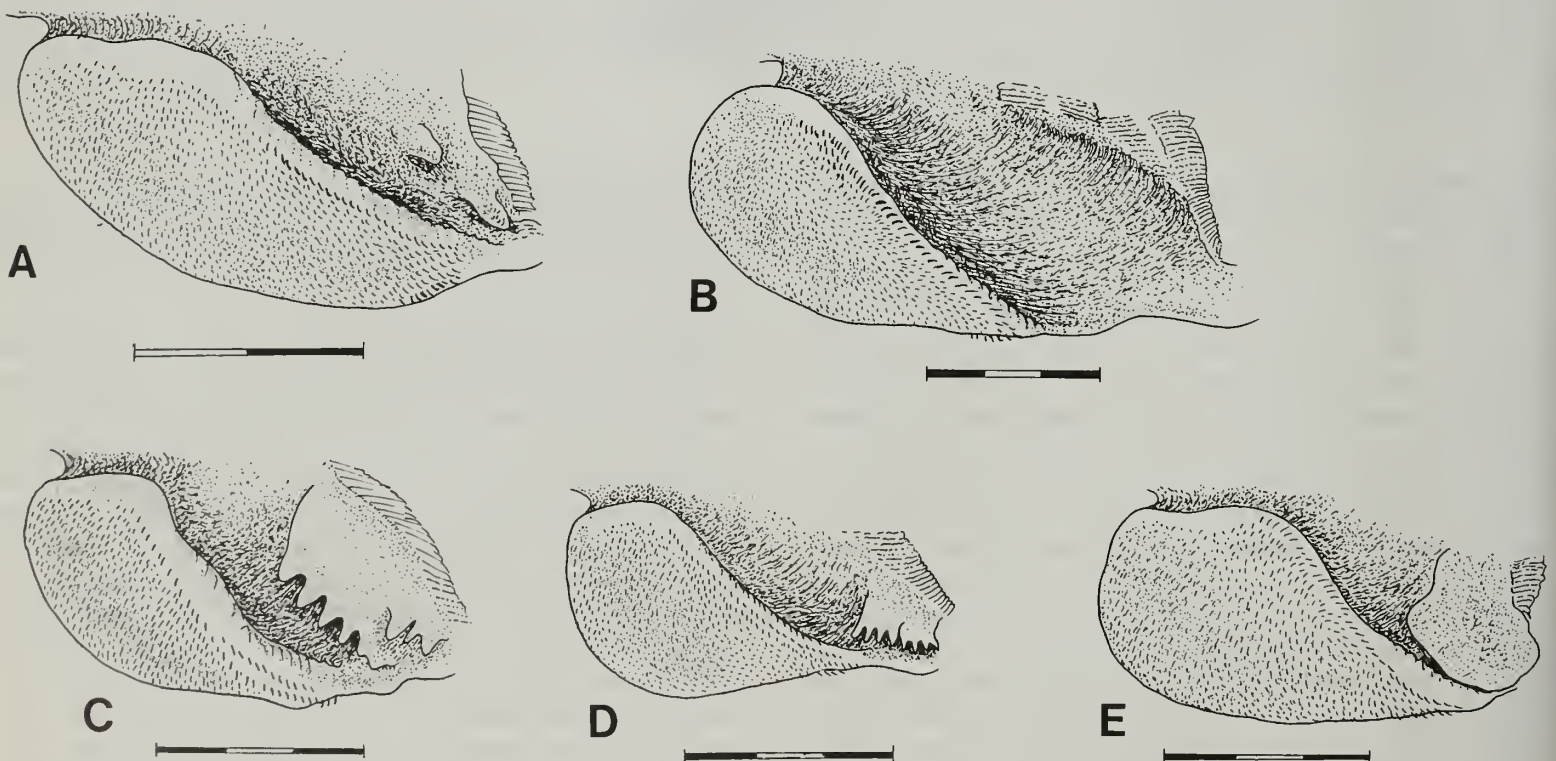

Fig. 17   PBO of A, *Mugil hospes* (BMNH 1975.10.7: 1–2, 156.5 mm SL); B, *M. thoburni* (1901.6.26: 170–1, 153 mm SL). Lateral views of right side.

Fig. 18   PBO of A, *Liza ramada* (PA 271186, 62 mm SL); B, *L. haematocheilus* (BMNH 1923.2.26: 248, 208 mm SL); C. *L. waigiensis* (1974.5.25. 3649–73, 90 mm SL); D, *L. grandisquamis* (1981.6.19: 198–202, 119 mm SL); E, *L. abu* (1968.12.13: 446–51, 110 mm SL). Lateral views of right side.

regarded *Mugil labiosus* Val. as a species of *Oedalechilus* which Schultz (1953) had made the type species of *Plicomugil*. There are, however, distinct differences in the PBO's, and in the nature of the lip folding, tooth shape and lower jaw shape between *O. labeo* and *O. labiosus* (p. 125). We thus accept *Plicomugil* as a valid genus to contain *O. labiosus* which exhibits the expanded denticulate area typical of the derived condition (node 5 on Fig. 20), (*cf. O. labeo*).

Mugil has a variable PBO morphology and among the species examined, five groups can be distinguished (see p. 125 for description of the features delimiting these groups), *viz*: 1) including *M. cephalus* (type species), *bananensis*, *curema*, *curvidens*, *incilis* and *trichodon*; 2) *M. capurii*, considered by Ingham (1952) the most primitive *Mugil* species (certainly the wide and shallow separation of the denticulate cushions and large proximal teeth are plesiomorphic features); 3) *M. liza* which more closely resembles *Liza* species; 4) *M. thoburni* and *M. setosus*, which are certainly closely related species and may represent the respective ends of a clinal distribution, the former in the Galapagos, the latter at the western coast of Mexico (Schultz (1946) recognised *Xenomugil* to contain *M. thorburni*); 5) *M. hospes*, which in the feature of its vertical sulcus most closely resembles *Neomyxus leuciscus*, but the overall PBO morphology and valve size suggests that it is a specialised variant of the *M. cephalus* group.

Now considering the advanced genera which exhibit the more plesiomorphic condition of a relatively small denticulate area (*ie.*, terminal group of Fig. 20), *Sicamugil* has a *Liza*-like PBO morphology although with specialised features (p. 124). Schultz (1946) synonymised *Sicamugil* with *Trachystoma* (=
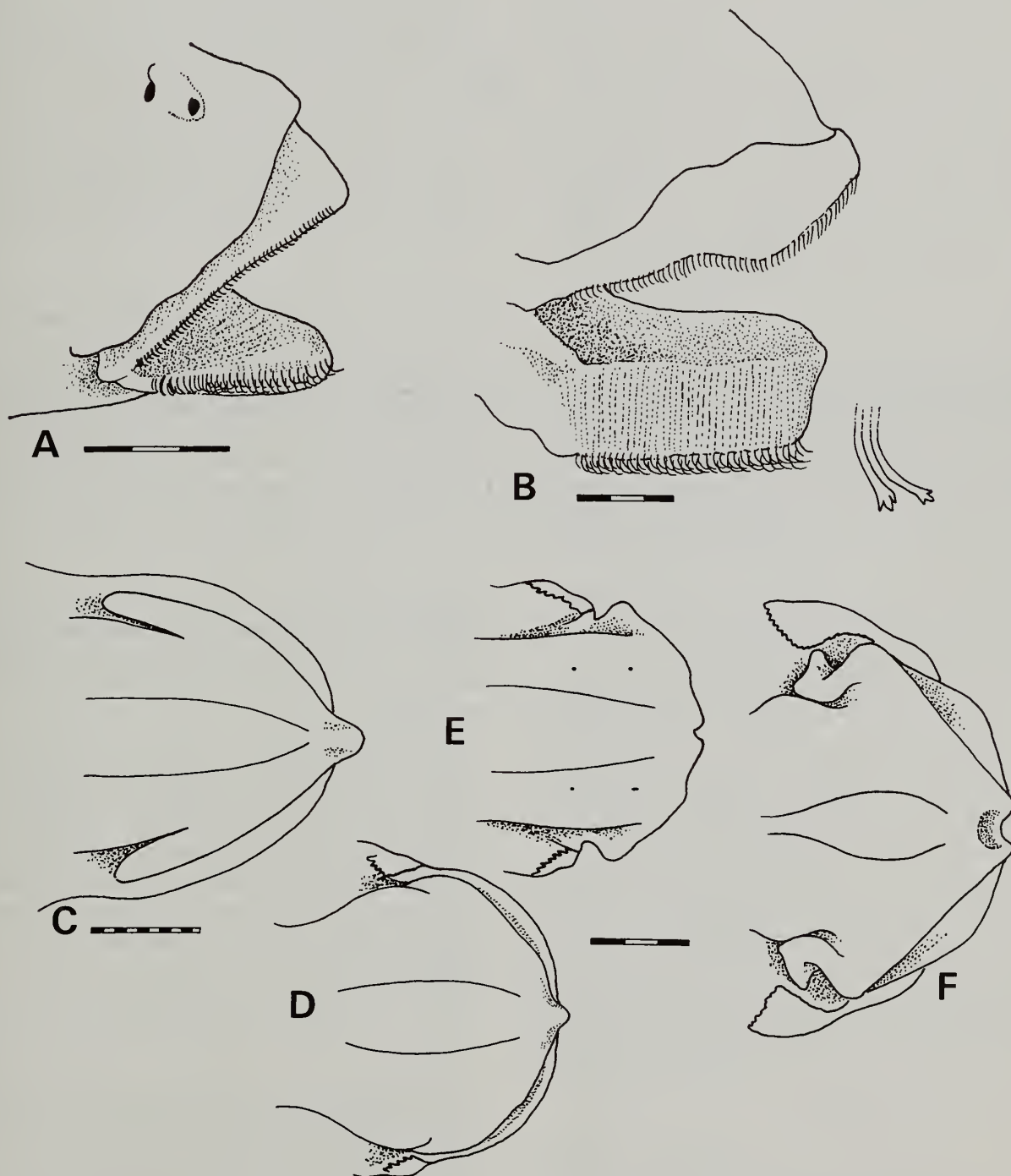

Fig. 19 Jaw dentition (lateral views) in A, *Chaenomugil proboscideus* (BMNH 1908.5.15: 178–9, 185 mm SL); B, *Neomyxus leuciscus* (1877.7.24: 13, 200 mm SL), the tips of the teeth are shown enlarged. Lower jaw shape (ventral views) of C, *Mugil capurii* (1933.2.28: 1–2); D, *Mugil curema* (1891.5.12: 33–42); E, *Liza abu* (1986.1.31: 1–3); F, *Liza waigiensis* 1974.5.25: 3649–73), a shape associated with a specialised PBO valve-type (see text).
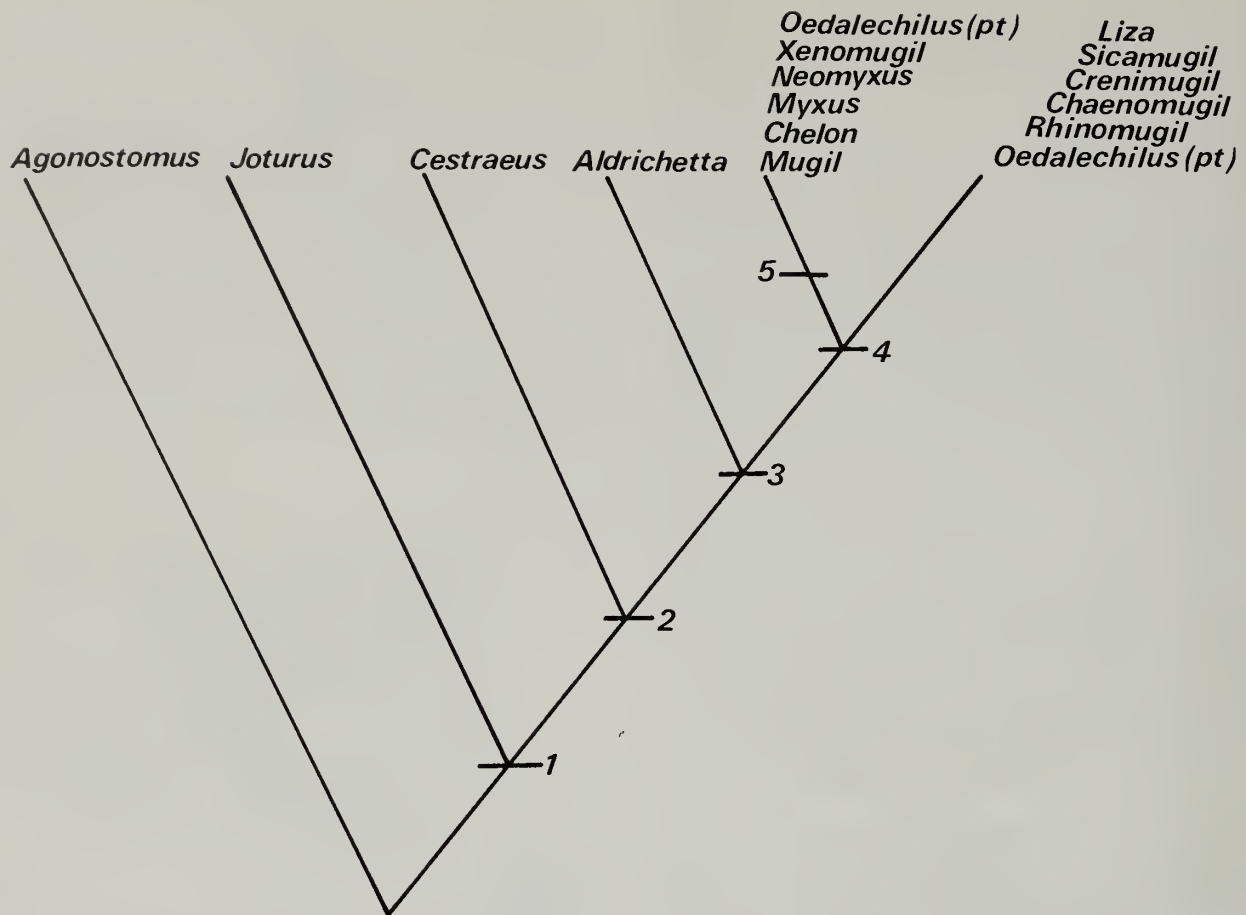
Fig. 20 Cladogram of mugilid genera based on pharyngobranchial organ synapomorphies, *viz*. 1) Development of rudimentary sulcus and fat body. 2) Majority of pharyngobranchial teeth are distal-type; partial attachment of *retractor dorsalis* muscle to basioccipital. 3) Sulcus and anterior fat-body well-developed; all teeth, apart from those on anteromedial area of 3rd toothplate are distal-type. 4) PBO completely developed with anterior and posterior fat-bodies, well-formed sulcus, enlarged, modified pharyngobranchial toothplates, teeth lost from pharyngobranchial 2; *retractor dorsalis* distinctly divided anteriorly into dorsal and ventral segments, the dorsal originating from the basioccipital. 5) Toothplates with outer margins vertically aligned; sulcus deep and narrow. Although several PBO apomorphies characterise taxa of these two lineages, none appear to be synapomorphic (see text).

Myxus; see above), but in lower jaw morphology *Sicamugil* appears to belong with those *Liza* species having a moderately developed denticulate area (see above).

Rhinomugil has a PBO morphology resembling that of *Liza*, in both the area and shape of its sulcus. Like many *Liza* it has an acute ventral profile to the lower jaw and differs only in its longer snout and wide separation of anterior and posterior nasal openings. *Squalomugil* Ogilby (type species *Mugil nasutus* De Vis) is a synonym (see Schultz, 1946).

Chaenomugil has a reduced denticulate area and extensive sulcus, features shared with a group of *Liza* species (p. 126). *Crenimugil* has PBO features and an angular lower jaw shape characteristic of *Liza*. Trewavas & Ingham (1972: 21) considered *Mugil heterochilus* and *M. macrochilus* to belong to the same 'evolutionary series' as *Crenimugil crenilabis* thus implying their inclusion in that genus. We find, however, that the PBO of *Mugil heterocheilus* more closely resembles that of *Liza* spp and refer it to that genus (p. 125). We have not seen a specimen of *M. macrocheilus*.

Liza species fall into three groups on PBO morphology; (1) the more speciose, exemplified by *L. ramada* (see p. 125 for other species, and characters delimiting this group), (2) differing from the first group in lacking valves, exemplified by *L. falcipinnis*, and possibly *L. haematocheilus* which also lacks valves but has a more extensive sulcus (p. 125), (3) characterised by a more reduced denticulate area and wide

sulcus. This latter group has a marked angular lower jaw shape (Fig. 19F). *Mugil liza* has a PBO morphotype typical of the *Liza ramada* group, except in having a single rather than a double valve in which respect it closely resembles *Liza abu* (p. 126).

The morphotype groupings of the PBO support, to a large extent, the present recognition of mugilid genera but at the same time indicate that the speciose genera *Liza* and *Mugil* are possibly non-monophyletic assemblages. Certainly there are species-specific PBO morphotypes (see above for examples in *Mugil* and *Liza*). Sulcus valve morphology is distinctive enough to categorise some groups of taxa (*eg.*, the crenulate type restricted to some *Liza* species; p. 125). We argue that these represent derived groupings since ontogenetically, valves originate from a double pharyngobranchial tissue fold similar to that present in adult *Joturus* (p. 124) which covers the area between the 2nd and 3rd pharyngobranchials. Absence of valves is also taken as a derived (loss) condition.

The distribution of the homologues discussed above and the groupings summarised in the cladogram (Fig. 20) might serve as a basis for re-diagnosing genera. Jordan & Evermann (1896) recognised *Agonostomus* as belonging to a separate subfamily and in a formal classification of our phylogenetic hypothesis this would be so. We recognise it as being the plesiomorphic lineage of other mugilids (p. 126). That the Mugilidae is, itself, a monophyletic group is amply borne out

by the derived nature of the upper gill-arch elements and their associated musculature; shared derived features of the lower gill-arch musculature indicate a sister-group relationship with atherinomorphs (Stiassny, 1990). Stiassny (1991) has also suggested an alternative relationship with 'higher percomorphs'.

In microphagous euteleosts a filtering pharyngeal organ is always developed from modifications to the epibranchials, noticeably involving hyperdevelopment of the 4th. Nelson (1967) reviewed the structure of the epibranchial organ among these fishes and concluded that such structures had not evolved in higher teleosts because an advanced structural organisation involving the *retractor dorsalis* muscle precludes such development. Nelson noted that the *retractor dorsalis* confers a manipulative role to the upper pharyngeals (pharyngobranchials) and that any specialisations of the upper gill-arches in higher teleosts involve the pharyngobranchials. The structural modifications to the upper gill-arches in Mugilidae have involved the unity and expansion of the 3rd pharyngobranchial and the 4th toothplate, and their manipulation has been refined by the division of the *retractor dorsalis* and the hypertrophy and forward shift of the 2nd *levator internus*. Unlike the euteleostean epibranchial organ, which is essentially an 'internal' structure whereby the posterior gill-arches are enclosed within a diverticulum, in mugilids the pharyngobranchial organ is an external structure with the gill-arches surrounding it.

A close parallel occurs between mugilids and the cyprinid *Hypophthalmichthys* in which the gill-arches surround the main body of the epibranchial organ which is manipulated by a forwardly directed and divided *adductor hyomandibularis* muscle (the functional homolgue of the 2nd *levator internus* of mugilids). *Hypophthalmichthys* differs from mugilids in having the epibranchials enclosed in internal ducts within the epibranchial organ, such that detrital material is filtered first externally and then passes into the organ for further processing (Howes, 1981). Mugilids, presumably because of the 'restriction' imposed by the *retractor dorsalis*, have not evolved an invaginated organ but have utilised that muscle to permit a degree of manipulation resulting in a highly selective trophic apparatus not available to the cyprinid.

Fine particulate matter is a richer source of adsorbed and absorbed nutrients than coarser material (Wood, 1964; Odum, 1968) and the majority of mugilids utilise such a resource with, perhaps, a capacity to be selective in the process (see functional discussion above). In so doing, mugilids exploit a resource unavailable to most other fishes and are largely freed from any competitive interaction, thereby permitting them to occupy habitats denied to other taxa (Hartley, 1940; Hickling, 1970; Odum, 1970; Capanna *et al.*, 1974). Moreover, mugilids being the fundamental harvesters in those communities, provide the agency for converting a low-grade unavailable resource into a high-grade available one (Hiatt, 1944; Odum, 1970; Brusle, 1981).

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